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Primary production and phytoplankton dynamics in western Lake Erie.

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PRIMARY PRODUCTION AND PHYTOPLANKTON DYNAMICS IN WESTERN LAKE ERIE

by

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Abstract

Primary production studies have had a profound impact on the management of the Great Lakes, culminating with the Great Lakes Water Quality Agreement of 1972 between Canada and the United States. The current study examined primary production and phytoplankton dynamics in western Lake Erie with application to water quality and fisheries management practices.

Annual primary production, estimated using a ^{14}carbon tracer and both *in situ* and constant light incubations, ranged from 320 – 370 g C m^{-2} y^{-1} during the study period and was similar to the 340 g C m^{-2} y^{-1} reported in the basin for 1970. Phytoplankton standing crop, measured as chlorophyll a, declined from annual mean concentrations of 11 mg m^{-3} in 1970 to 4 – 7 mg m^{-3} in this study. The mean fresh-weight biomass of the phytoplankton standing crop for spring and summer ranged from 5 – 7 g m^{-3} in 1970 to current estimates of 4 - 5 g m^{-3}. Taxonomic analysis of the phytoplankton community revealed the presence of more oligotrophic genera (e.g. *Chlamydomonas*, *Cyclotella*, *Microcystis*) than in 1970.

Summer mean carbon turnover rates, measured as a function of primary production and Chlorophyll a, have doubled from 4.5 days in 1970 to 2 days. Furthermore, upwards to 35% of the entire lake's primary production would be required to support a fishery composed of top predators. It is proposed that regular measurements of primary production be integrated into both water quality and fisheries management.

Dedication

This work is dedicated to my wife Wendy, to my parents Murray and Maureen, and to my parents-in-law Gary and Diane, to whom I owe an enormous debt of gratitude. Of course, I also owe them an apology.

Acknowledgements

I would like to thank my committee members, Dr. G.D. Haffner, Dr. M. Munawar, Dr. J.H. Leach, Dr. H.J. MacIsaac and Dr. D. Fowle for their support and guidance. I would also like to thank Dr. T.B. Johnson and the staff of the Ontario Ministry of Natural Resources Lake Erie Management Unit for their operational and academic support. Special thanks are due to T. Leadley, K. Drouillard, H. Hagen, M. Cook, S. Wood, V. Lee, H. Niblock and S. Carou for their help in all stages of the research. Finally, I would like to thank all of the staff and students at the Department of Biology and Great Lakes Institute for Environmental Research for enriching this experience.

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Introduction

Overview

Aquatic primary productivity is the conversion of radiant energy into chemical energy, and therefore sets the limits of biological production in aquatic ecosystems. Despite the importance of knowing the production limits of the Great Lakes, primary productivity studies have been neglected as a critical component of Great Lakes research for the last 35 years. Only one complete set of studies, 7 in total, has been implemented to quantify primary production throughout the Great Lakes (Olson and Odlaug, 1966; Parkos et al. 1969; Schleske and Callender, 1970; Fee, 1971; Glooschenko et al. 1973; 1974a and Stadelmann et al. 1974) since the late 1960s, and all studies were focused on eutrophication issues. Eutrophic lakes are characterized by: high nutrient levels, high algal growth rates, and increased rates of oxygen depletion. In the Great Lakes, eutrophic conditions were attributed to widespread environmental degradation (International Joint Commission (IJC), 1969). These observations led to the Great Lakes Water Quality Agreement (GLWQA) signed in 1972 between Canada and the United States (IJC, 1974) and affects the daily lives of 35 million people. During the implementation of the GLWQA, primary production studies were abandoned despite the 'ecosystem approach' endorsed for managing the Great Lakes.

The Great Lakes support a sport fishery worth $4 billion per annum (U.S. NOAA, 2002). Recent studies have attempted to quantify the link between primary production and sustainable fisheries both globally (Pauley and Christensen, 1995) and within the Great Lakes (Sprules et al. 1999). Both studies reached a similar conclusion: that measured

levels of primary production were not sufficient to support the respective food webs. These food webs, however, continue to support significant fisheries making it quite evident that primary production is poorly understood. The link between primary production and water quality management objectives was explicitly defined in the GLWQA, and has been implicitly recognized in recent food web models, but few studies were ever undertaken. Primary production has also been shown to have a critical role in regulating the impact of toxic chemicals (Epplett et al. 2000). Understanding carbon flow dynamics in aquatic food webs is essential for managing aquatic ecosystems. The need for information on the factors that regulate primary production and organic carbon dynamics in aquatic food webs is the rationale for undertaking primary production studies of the western basin of Lake Erie.

Primary production is defined as the energetic contribution of all photosynthesizing organisms, specifically plants and algae, to the ecosystem over a specific period of time and primary productivity is defined as the rate of energy fixation per unit time (Smith, 1992). The distinction between these terms is often confused in the literature (e.g. Glooschenko et al. 1974a; Wallen and Botek, 1984; Munawar and Munawar, 1999). For the sake of clarity, in this study primary productivity refers to the volumetric rate of carbon uptake in one hour, i.e. mg C m^{-3} h^{-1} (Munawar and Munawar, 1999), and primary production refers to the water column rate of carbon uptake per day or per annum, i.e. g C m^{-2} d^{-1} (Glooschenko et al. 1974a) or g C m^{-2} y^{-1} (Vollenweider et al. 1974).

Although the sources that contribute to primary production include benthic algae and macrophytes, pelagic algae or phytoplankton, are the focus of this study. References to

primary production refer specifically to phytoplankton primary production. Similarly, references to algal biomass specifically refer to phytoplankton biomass. This study therefore addresses the changes in phytoplankton dynamics in the western basin of Lake Erie since 1970 and provides a new perspective based on organic carbon budgets on resource management.

Literature review

The western basin of Lake Erie supports the world's largest commercial freshwater fishery. Recent declines in some of the more important species such as rainbow smelt (*Osmerus mordax*) and yellow perch (*Perca flavescens*) (MacGregor, 1999) and fluctuations in walleye (*Stizostedion vitreum*) harvests (Nepszy, 1999) have raised concerns about the sustainability of the commercial and sport fisheries of Lake Erie. In the 1960s, there was evidence that Lake Erie was becoming eutrophic. Specifically, benthic algal blooms (*Chladophora sp.*) in nutrient rich nearshore areas caught the public's attention and were observed throughout many of the Great Lakes (Vallentyne, 1974). Anoxia was also occurring in the hypolimnion of the central basin of Lake Erie (Burns and Ross, 1972), making conditions unsuitable for many species. It was at this time that the mayfly (*Hexagenia limbata*) disappeared from the western basin (Carr and Hiltunen, 1965). The GLWQA implemented a phosphorus management strategy to alleviate eutrophication. By limiting phosphorus inputs, it was anticipated that primary production would in turn be limited and that algal biomass would decline.

The scientific rationale underlying the GLWQA has been reviewed extensively in Vollenweider et al. (1974). Two empirical models (reproduced in Figure 1) were

proposed as the pre-eminent management tool for controlling eutrophication. The first model (Fig. 1a) quantifies the relationship between phosphorus loadings and annual primary production. The second model (Fig. 1b) quantifies the relationship between algal biomass (measured as chlorophyll a) and annual primary production. These models defined trophic status (i.e. oligotrophic, mesotrophic and eutrophic) as a function of the three parameters, and represent eutrophication as a function of high phosphorus loadings, high primary production and high algal biomass, and predicted that eutrophication would be alleviated by the restriction of phosphorus loadings.

By incorporating the primary production data of the seven previously cited studies, along with previously published chlorophyll a measurements (Glooschenko et al. 1972; 1973; 1974b; Fee, 1971; Robertson et al. 1971) and including new estimates of phosphorus loadings, Vollenweider et al. (1974) used these empirical models to conclude that the western basin of Lake Erie was eutrophic and that the central and eastern basins along with Lake Ontario were in the process of eutrophication. A binational approach to the management of phosphorus was identified as the best option to reverse this trend towards eutrophication.

In the early 1980s, phosphorus controls were concluded to be working. By deploying the phytoplankton species *Fragilaria crotonensis* as a bioindicator, Hartig (1985) reported significant declines in its density in western Lake Erie between 1977 and 1982, coincident with the phosphorus control measures of the GLWQA taking effect. Similarly, Nicholls and Hopkins (1993) reported steady declines in both phosphorus loadings and

phytoplankton densities in the western basin between 1978 and 1987. Both studies indicated that nutrient controls were working as intended.

It would be a gross misrepresentation of Nicholls and Hopkins (1993) work, however, to use it only in this context. For it was also shown in this study that between 1988 and 1990, phosphorus loadings increased as phytoplankton densities declined exponentially. This decrease in phytoplankton densities corresponded with the establishment of the exotic zebra mussel (*Dreissena polymorpha*) in the basin in 1988. The implication was that zebra mussels were controlling algal standing crops and thus uncoupled the tight relationship between algal biomass and phosphorus loadings. If true, this would have far reaching implications for the GLWQA.

Throughout the 1990s, a large body of research supported the observation that the zebra mussel and the closely related quagga mussel (*Dreissena bugensis*) were having dramatic impacts on the phytoplankton community (e.g. Nicholls and Hopkins, 1993; Madenjian, 1995; Berg et al. 1996; Dermott and Munawar, 1993; Munawar and Munawar, 1996; 1999; Stoekmann and Garton, 1997; Makarewicz et al. 1999). Zebra mussels had the potential to filter approximately 20% of the water column each day (MacIsaac et al. 1992), and it was suspected that they were selectively feeding on diatoms (Dermott and Munawar, 1993; Dermott et al. 1998), which would greatly alter the composition of the phytoplankton community. Munawar and Munawar (1996;1999) and Makarewicz et al. (1999) reported significant declines in phytoplankton biomass after the establishment of exotic mussels in the basin showing general agreement with Nicholls and Hopkins (1993) observations that zebra mussels were likely regulating the standing crop. Furthermore,

Munawar and Munawar (1999) reported a significant change in the structure of the phytoplankton community, with Chlorophyta replacing Diatomeae as the dominant taxa. This was consistent with the basin becoming more mesotrophic and less eutrophic (Munawar et al. 2002), the goal of the GLWQA. However, Makarewicz et al. (1999) reported that diatoms were still the most commonly occurring taxa in the spring and summer seasons of 1989-1993.

Nicholls et al. (1999a) concluded that exotic mussels were removing approximately 6000 tonnes per year of phosphorus from Lake Erie. By comparison, the GLWQA recommended loadings of 8000 tonnes per year. In another study, the same authors (Nicholls et al. 1999b) reported that chlorophyll a to total phosphorus ratios declined sharply with the establishment of the zebra mussel in the western basin, and argued that the chlorophyll / phosphorus relationship inherent to Vollenweider's models had become uncoupled. These conclusions were in contrast to Charlton et al. (1999) and Charlton and Milne (*in press*) whose independent examination of chlorophyll a to total phosphorus ratios revealed no significant decline between1968 and 1997 and noted that the sharpest drop corresponded with the onset of nutrient controls.

There is some agreement in the literature on the impacts of reduced phosphorus loadings and exotic mussels on phytoplankton biomass, but there is little agreement on their interactions and collective impacts. More importantly, while virtually all of the studies reviewed here have suggested that there are significant consequences for the management of Lake Erie with respect to current provisions of the GLWQA and more specifically the

use of Vollenweider et al.'s (1974) empirical models in managing phosphorus loads, none have actually incorporated these models into the their research.

This lack of understanding as to the factors that regulate primary productivity in the lake becomes even more poignant with an examination of primary production research in the western basin. Munawar et al. (1999) reported a tenfold decline in primary productivity (i.e. the volumetric rate, in mg C m^{-3} hr^{-1}, of primary production) between the spring of 1988 before the establishment of zebra mussels and 1993, a trend which continued throughout the 1990s. The implication was that the level of primary production had also declined well below that predicted by the nutrient control models. Of the studies that considered primary production, Dahl et al. (1995), whose data were incorporated into the work of Sprules et al. (1999), did not consider how the observed production estimates related to the original Vollenweider models.

Dahl et al. (1995) concluded that seasonal weighted mean primary production (calculated from May to October data) declined from 228 g C m^{-2} in 1983-85 to 146 g C m^{-2} in 1993. Only the 1993 data, however, were actually measured. The 1983-85 values were estimated from a model developed for the Bay of Quinte, Lake Ontario (Millard et al. 1996) and should be considered with some trepidation.

Sprules et al. (1999) estimated that the energy requirements of zebra mussels from 1993-1996 were approximately 11 times greater than the available primary production, and the energy requirement of the entire food web was approximately 13 times greater than the

available primary production. The annual primary production used in the Sprules model is roughly 290 g C m^{-2} y^{-1} with the energy requirement of the food web being roughly 3 770 g C m^{-2} y^{-1}. By comparison, the theoretical maximum value of primary production for any temperate body of water established by Vollenweider et al. (1974) is 420 g C m^{-2} y^{-1}. The Sprules and Vollenweider models are not necessarily incongruous in that besides pelagic productivity, organic carbon supplies include other autochthonous sources (benthic primary production, macrophytes) and allocthonous sources (sewage treatment plants and detrital organic matter contained in runoff) from the watershed.

Despite this apparent discrepancy in the organic carbon budget of Lake Erie, an overall portrait of post - nutrient control and post - zebra mussel phytoplankton dynamics in the western basin began to emerge. Phytoplankton standing crop, measured as fresh weight biomass (g m^{-3}) (e.g. Munawar and Munawar, 1996; 1999; Makarewicz et al. 1999), density (ASU ml^{-1}) (e.g. Nicholls and Hopkins, 1993) or chlorophyll a (mg m^{-3}) (e.g. Nicholls et al. 1999b; Charlton et al. 1999) has shown substantial declines and there is evidence that grazing by exotic mussels may be reshaping the phytoplankton community (Dermott and Munawar, 1993; Dermott et al. 1998; Munawar and Munawar, 1999). There is further evidence to suggest that the phosphorus to chlorophyll relationship has become uncoupled since the arrival of the zebra mussels in the lower Great Lakes (Nicholls et al. 1999b), although this suggestion is challenged by the findings of Charlton et al. (1999) in western Lake Erie. Furthermore, there is evidence to suggest that primary productivity has declined by an order of magnitude (Munawar et al. 1999) and that primary production levels are more than an order of magnitude less than required to sustain the food web (Sprules et al. 1999). These production data indicate that there may

be serious problems with the continued use of Vollenweider's models as management tools in the Great Lakes. Estimates of *in situ* primary production, however, are essential for the management of both fisheries and water quality in Lake Erie and have not been established by current monitoring and research programs.

The GLWQA was implemented to ensure the future health of the ecosystem, something that was in doubt with the onset of eutrophication and the decline in prized fish stocks. A healthy ecosystem is one where the fish maintain sustainable populations and are safe for human consumption and not contaminated with toxic chemicals. This was recognized in the 1978 revisions to the GLWQA (IJC, 1988). Western Lake Erie receives high levels of sediment bound contaminants (Carter and Hites, 1992) but shows fewer signs of toxic stress than other areas of the Great Lakes (Weseloh et al. 1992). This situation has been attributed to trophic dilution (Haffner and Koslowski, 1999; Epplett et al. 2000), a process where high levels of primary production relative to the standing crop are minimizing toxic effects by restricting chemical partitioning between the phytoplankton and the sediments.

Very little attention has been given to the role of primary production in sustaining healthy fisheries. Independent estimates of annual primary production from Vollenweider et al. (1974) and annual fish production from Leach et al. (1987) revealed that in Lake Erie during the 1970s, primary production was almost 600 times greater than that of large (>1000 g) sport fish. Munawar et al. (1999) attributed a strong mixture of netplankton, nanoplankton and picoplankton productivity in western Lake Erie to the relatively healthy state of the fishery in 1998. Sprules et al. (1999), however, indicated that primary

production was not supplying enough energy to support the food web in Lake Erie. A model similar to that developed by Pauley and Christensen (1995) which estimates the primary production required to support a fishery based on global catch data, will be developed in this study.

Objectives

Aquatic primary production is the common thread that integrates research on multiple stressors such as eutrophication, sustainable fisheries, species invasions and contaminant dynamics. Primary production regulates the energy budgets and flows of aquatic ecosystems. Thus an understanding of the primary production regime is critical to managing and maintaining ecosystem health. This study will monitor five basic parameters in western Lake Erie: primary productivity (mg C m^{-3} hr^{-1}), phytoplankton biomass (g m^{-3}) and taxonomy, chlorophyll a (mg m^{-3}), total phosphorus (mg l^{-1}) and nitrogen (nitrate) (mg l^{-1}). From these data, changes in primary production, phytoplankton standing crop, autochthonous carbon and nutrient dynamics are interpreted with respect to observations from previous studies and current fisheries issues.

Previous studies in western Lake Erie have used different techniques for estimating primary productivity. The basic method used is a ^{14}carbon tracer to estimate carbon uptake (Steeman-Nielsen, 1951) although there are considerable differences in the method of incubation. *In situ* incubations (Glooschenko et al. 1974a), constant light incubators (Glooschenko et al. 1974a; Munawar and Munawar, 1999) and variable light incubators (Wallen and Botek, 1984; Dahl et al. 1995) have been used. This study

compares *in situ* with constant light incubations in order to facilitate the integration of these long-term data sets.

This study specifically probes changes in phytoplankton dynamics of western Lake Erie since 1970 by addressing the following questions:

- How has the standing crop of phytoplankton changed with respect to biomass and community structure? This assessment will include a discussion of changes in the underwater light regime and levels of growth limiting nutrients, nitrogen and phosphorus, since the imposition of nutrient controls.
- Are current levels of primary production and chlorophyll a consistent with the models developed by Vollenweider et al. (1974) and incorporated into the GLWQA?
- Have autochthonous carbon dynamics changed since the imposition of nutrient controls?
- Is the current level of primary production sufficient to sustain the commercial fishery?

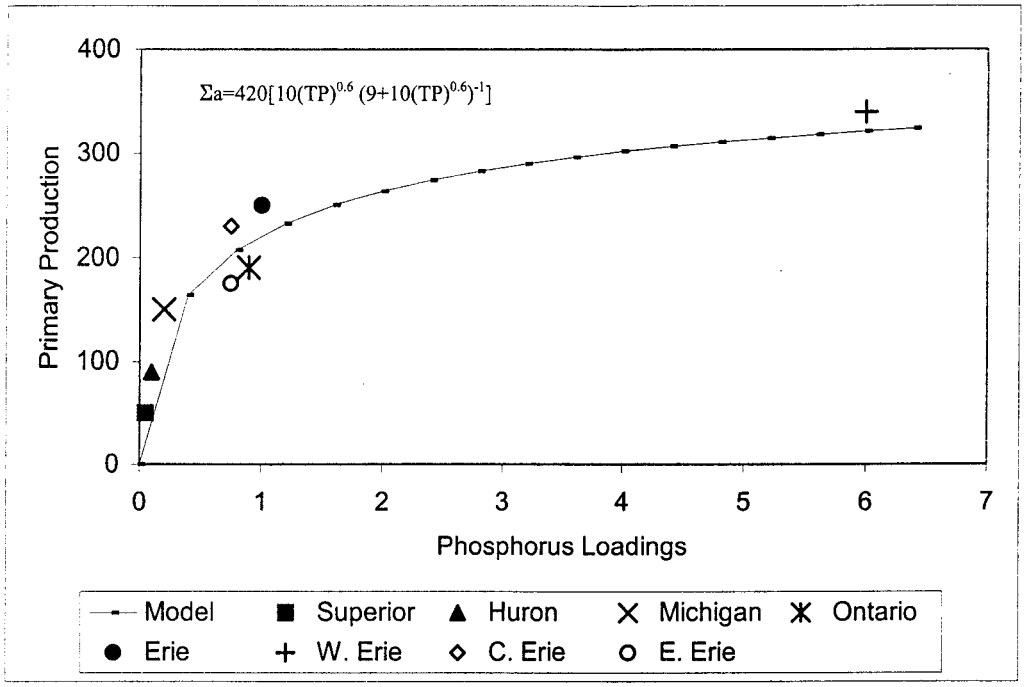


Figure 1a: Relationship between annual primary production (g C m^{-2} y^{-1}) and annual phosphorus loadings (g TP m^{-2} y^{-1}). Reproduced from Vollenweider et al. (1974).

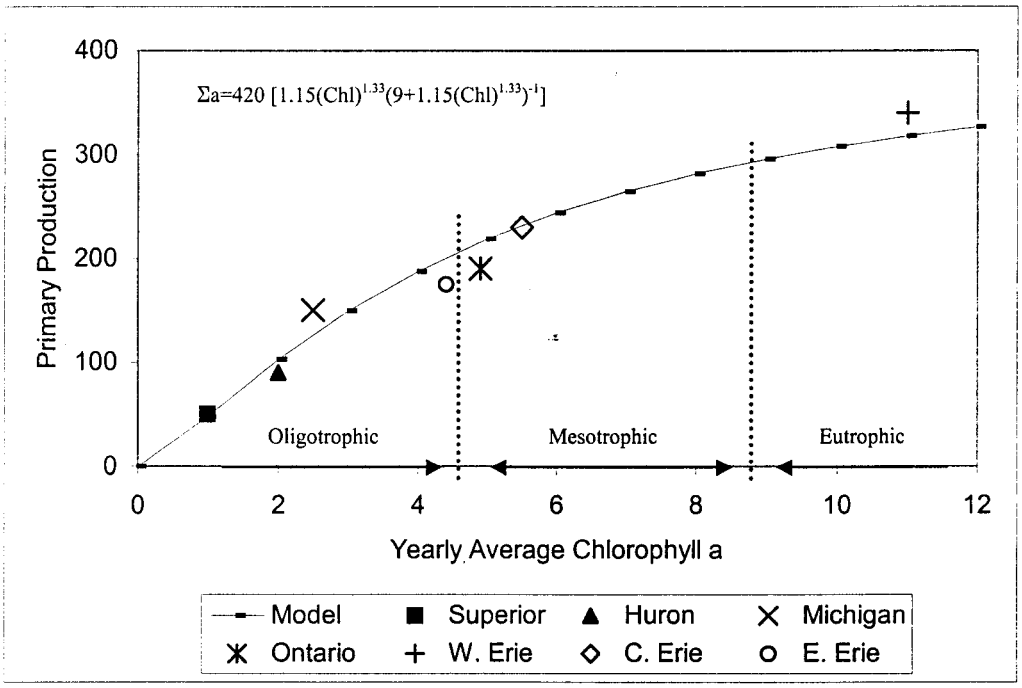


Figure 1b: Relationship between annual primary production (g C m^{-2} y^{-1}) and surface chlorophyll a concentrations (mg m^{-3}). Reproduced from Vollenweider et al. (1974).

Materials and Methods

Study Area

Lake Erie is the southernmost of the Laurentian Great Lakes and the western basin comprises 2 912 km^2 of the total 25 320 km^2 (Schertzer, 1999). The western basin is bordered by the Province of Ontario to the north, and by the States of Michigan and Ohio to the west and south. Figure 2 illustrates the five sampling sites in the northern (Canadian) portion of the basin that were chosen for study: Middle Sister Island (MSI), W5, W6, W7 and W8. The exact locations are **MSI**: N 41^0 49.51, W 82^0 59.21; **W5**: N 41^0 59.20, W 82^0 34.50; **W6**: N 41^0 53.00, W 82^0 36.80; **W7**: N 41^0 59.50, W 82^0 45.80; **W8**: N 41^0 51.25, W 82^0 45.80.

Sampling Program

Two distinct sampling regiments were undertaken; the first at MSI measured *in situ* primary productivity, and the second at sites W5, W6, W7 and W8 measured size fraction contributions to productivity using a constant light incubator.

1. At MSI, discrete depth water samples were collected using a 2L "Kemmerer" water bottle at 0, 1, 3, and 5 metres for each cruise during 2000 and at 0, 1, 3, 5 and 7 metres for each cruise during 2001 and 2002. From each sampled depth, subsamples were extracted shipboard for estimates of primary productivity, phytoplankton taxonomy and biomass, total phosphorus and nitrate. Phytoplankton and nutrient samples were stored in coolers and transported to University of Windsor, Great Lakes Institute for Environmental Research (GLIER) for analysis. Measurements of irradiance, temperature, dissolved

oxygen, specific conductivity, reduction potential (redox) and pH were also recorded using a LiCor Quanta Meter and a Hydrolab Surveyor System.

2. At W5, W6, W7 and W8, one 'integrated' (Fee, 1976) water column sample was collected and stored in an insulated Nalgene carbuoy and transported to the Ontario Ministry of Natural Resources (MNR) laboratory at Wheatley, Ontario where subsamples were drawn for measurements of primary productivity, chlorophyll a, total phosphorus and nitrates. Water column irradiance levels were recorded at W5 and W8.

Methods

Temperature, dissolved oxygen, specific conductivity, reduction potential and pH

Temperature, dissolved oxygen, specific conductivity and reduction potential and pH were measured at MSI using a Hydrolab DataSonde 4a Surveyor at 1m intervals throughout the water column from the surface to 8 metres. The Hydrolab surveyor was calibrated prior to the start of each field season in accordance with the manufacturer's specifications.

Irradiance, euphotic depth and vertical attenuation

Irradiance in the water column was measured using a Li-Cor Spherical Quantum Sensor attached to an LI-1000 Data Logger at 1 metre intervals from the surface to 8 metres.

Euphotic depth, Z_{eu}, is the theoretical depth in the water column where photosynthesis ceases and is assumed to be 1% of the surface value (I_0), such that:

$I_{Zeu} = 0.01\ I_0$, where

I_{Zeu} = Irradiance at euphotic depth

I_0 = Irradiance at the surface.

Z_{eu} was calculated for each cruise at MSI, W5 and W8 by logarithmic regression of the Irradiance vs. Depth curve. Where the calculated value exceeded the depth of the water column at 10 m, Z_{eu} was assumed to be 10 m.

The vertical attenuation coefficient, ϵ_{par}, the rate of decline of light intensity through the water column, was calculated from the equation:

$\epsilon_{par} = (\ln I_0 - \ln I_z)\ z^{-1}$ where

I_0 = surface irradiance

I_z = Irradiance at depth z.

Total Phosphorus

Total phosphorus (unfiltered) concentrations for the year 2000 were determined at sites W5 and W8 by staff at Environment Canada using a Brann and Luebbe AA3 Autoanalyser following the automated ascorbic acid technique (Eaton et al. 1995). For 2001, concentrations at MSI, W5, W6, W7 and W8 were determined using the stannous chloride method (ibid). Analysis was performed at the University of Windsor, Dept. of Biological Sciences, on a Beckman DU-530 Spectrophotometer. Samples at W5 and W8 were run concurrently at Environment Canada between May and September 2001 and used for comparison. In 2002, total phosphorus concentrations were determined at MSI, by GLIER staff following the same procedures as Environment Canada.

Nitrates

Nitrate levels were measured in 2000 and 2001 at W5, W6, W7, W8 and MSI were determined according to the colorimetric method (Eaton et al. 1995). All analyses were performed at the University of Windsor, Dept. of Biological Sciences on a Brann and Luebbe AA3 Autoanalyser. The same method was used on 2002 samples at MSI, by staff at GLIER.

Phytoplankton identification, enumeration and biomass

A 250 ml sample was collected from each depth at MSI and preserved immediately with 5 ml of Lugol's Iodine. Amber 'Boston' round bottles were used for storage to prevent photodegradation over time.

A modified version of the inverted microscope technique first developed by Utermohl (1958) was used to identify the phytoplankton samples. This is the most common technique used in Great Lakes research (Munawar and Munawar, 1996). Each sample was mixed thoroughly for 60 seconds and a 2 ml subsample was drawn and placed in a settling chamber for at least 4 hours to allow the phytoplankton to settle onto a slide. After settling, nascent water was drained as the top portion of the chamber was carefully removed and replaced with a cover slip. Slides were then ready for microscopic analysis.

Identification and counting were done using a Leica DM IRB microscope under 400X magnification. Taxonomic identification was carried out to the *genus* level using Tiffany (1934), Prescott (1962; 1970) and Lee (1999) as references. Counting procedures

followed Lund, Kipling and LeCren (1958). In each field, all phytoplankton were identified and counted. On each slide, 1 transect (approximately 80 fields) was counted. Counting of any particular genus was halted after 100 observations and in general, a minimum number of 16 organisms were counted. It was not always possible to meet this number even when more fields were surveyed, however, these counts were still included because these cells tended to be larger and thus represented a significant portion of the biomass (Munawar and Munawar, 1996).

Phytoplankton genera vary greatly in size between individuals and over time. Mean volumes for each observed genera were developed over two sampling seasons in accordance with Nauwerck (1963). Typically the dimensions of four random individuals were measured in ocular units from each cruise in which they were observed. A stage micrometer was used to convert ocular units into micrometers (μm). Since only two dimensions can be observed under the microscope and volume is a three dimensional quantity, width was assumed to equal depth. Over the course of two sampling seasons, 50-60 individuals were measured from each of the commonly occurring genera. Less commonly occurring individuals were measured as encountered. Calculation of biovolume for each genus was based on a standard geometric shape. Biovolume, in this study, was determined from the standardized shapes of Hillebrand et al. (1999). Table 1 shows mean biovolumes of phytoplankton genera counted in this study. The count multiplied by the standard volume yields the biovolume per genus per date.

Phytoplankton biomass was estimated by converting measurements of biovolume to fresh weight using the equation of Strickland (1960), which assumes that the specific gravity of phytoplankton is equal to 1, and therefore 10^9 μm^3 of phytoplankton have a mass of 1 mg.

Chlorophyll a and Organic carbon

Chlorophyll a estimates at sites W5, W6, W7 and W8 in 2000 and 2001 were determined by first filtering samples through Whatman GF/C filters and then using acetone pigment extraction and spectrophotometric analysis (Strickland and Parsons, 1968; Eaton et al. 1995). These measurements were performed by technicians of the Ontario Ministry of Natural Resources and were used in this study with their permission.

Chlorophyll a estimates for 2002 were made from samples collected at MSI at discrete depths. The filtering, acetone extraction and spectophotometric procedure adhere to Strickland and Parsons (1968) and was similar to the method employed by MNR.

Organic Carbon was determined from Chlorophyll a measurements using a Chlorophyll a to Carbon ratio of 40 (e.g. Strickland, 1960; Geider, 1987)

Primary Productivity

Two methods for estimating primary productivity were deployed in this study, the Light and Dark Bottle (LDB) method and the Size Fractionated Productivity (SFP) method. Both are similar in that a ^{14}carbon tracer is used to measure carbon uptake by the photosynthesizing algae. They differ mainly in that LDB samples, after being inoculated, are placed back in the water column to photosynthesize *in situ* whereas SFP samples are

placed in a constant light incubator. The ^{14}C tracer was contained in a buffer solution of pH 9 with an activity of 10 μCi $ml^{-1}$and was prepared in accordance with Vollenweider (1974).

Light and Dark Bottle Method (LDB)

This method was performed on the discrete depth water samples collected at MSI. The general procedures were outlined in Strickland and Parsons (1968), Vollenweider (1974) and Eaton et al. (1995). At each depth, two clear 300 ml B.O.D. bottles and one black 300 ml B.O.D. bottle were filled to just less than overflowing. Each bottle was then inoculated with 1 ml of ^{14}C buffer solution (10 μCi), mixed thoroughly and sealed. All bottles were then attached to a floating rack and placed in the water, so that the bottles were sitting at the depth they were sampled from and exposed to incipient light and temperature conditions. Samples were left in the water for 2-4 hours based on the amount of sunlight at the time of incubation, and when removed, were placed in a dark, sealed cooler for transport to the laboratory. Every effort was made to minimize the exposure time of the samples to surface light levels. At the lab, samples were processed in a darkened room. Exactly 200 ml from each bottle was filtered onto a Whatman *nucleopore* 0.45 μm polycarbonate filter; the filter was then rinsed with 0.01N hydrochloric acid (HCl) to remove any carbonate material that might have precipitated the ^{14}C, and the filter was then removed and placed in a 20 ml scintillation vial. 10 ml of Ultima Gold Scintillation fluid was added to each vial and radioactivity was counted on a Beckman LS 6500 Scintillation Counter.

Primary productivity (mg C m^{-3} h^{-1}) was calculated for each sampled depth using the equation of Vollenweider (1974):

$P = C^{14}_{upt} \times C^{12}_{avail} \times 1.06$ where

C^{14}_{upt} = net carbon^{14} uptake

C^{12}_{avail} = carbon^{12} available for uptake = 21 mg C l^{-1} (Vollenweider, 1974; Glooschenko et al. 1974; Munawar et al. 1999; MacDougall et al. 2001)

1.06 = isotope correction factor

Measurements were normalized for volume (m^3) and time (h). Average water column productivity was calculated by taking the weighted mean from the surface to the euphotic depth. Productivity to the euphotic depth was estimated from logarithmic, exponential or polynomial regression of the productivity vs. depth curve.

Size Fractionated Productivity (SFP)

The SFP technique was deployed on the integrated water samples collected from sites W5, W6, W7 and W8, as described by Munawar and Munawar (1986; 1996) and in McDougall et al. (2001). A 200 ml subsample from each site was inoculated with 1 ml of ^{14}C buffer solution (10 μCi), mixed thoroughly and then divided into 4 subsamples of 50 ml each in 200 ml Nalgene polycarbonate Erlenmeyer flasks and sealed. Subsamples were then placed in a constant light incubator for 4 hours and exposed to light levels of approximately 8000 lx, which was assumed to be equivalent to irradiance at light optimum. Incubator temperature was set within 3° C of the surface water temperature.

After incubation, 1 ml of sample water from each flask was extracted and placed in a 20 ml scintillation vial with 250 µl of ethanolamine to determine the total activity of the sample. The remaining 49 ml of sample were passed through a 20 µm Nitex mesh filter and a 2.0 µm Whatman *nucleopore* polycarbonate filter. The 2.0 µm filter was rinsed with 10% HCl, then removed and placed in a scintillation vial to determine the productivity of the 2-20 µm size class. The remaining sample was passed through a Whatman *nucleopore* 0.45 µm polycarbonate filter and this filter was again rinsed with 10% HCl, removed and placed in scintillation vial to determine the <2 µm size class productivity. Finally, the 20 µm Nitex filter was back rinsed over a 0.45 µm filter, rinsed with HCl, removed and stored in a scintillation vial to determine the >20 µm size class productivity. As with the LDB method, 10 ml of Scintillation fluid were added to each vial and radioactivity was counted on a Beckman LS-6500 Liquid Scintillation Counter.

Primary productivity for each size fraction was then determined using the equation of Vollenweider (1974) as with the LDB technique. Because an integrated sample was used, these values were assumed to represent an average for the water column. An average water column productivity rate was determined by simply adding the rates of the three size fractions together. This approach may under-represent the true water column productivity rate due to cell breakage during the filtration process.

Primary Production

Daily rates of primary production (mg C m^{-2} d^{-1}) were determined by multiplying the average water column productivity rate by the euphotic depth and by day length. For the

sake of consistency with other studies in the basin (Glooschenko et al. 1974, Dahl et al. 1995), day length was assumed to be 10 hours.

Annual rates of primary production (mg C m^{-2} y^{-1}) were estimated by calculating the average daily production rate within each season, and then multiplying the seasonal daily average by the length of the season (i.e. 91.25 days). Estimates of seasonal primary production were then added together to approximate annual primary production. This was similar in form to the depth – integrated primary production models of Vollenweider (1969) and Fee (1977) adjusted for the limnology of western Lake Erie.

Samples were not collected throughout the year, however, and an adjustment was required to produce an estimate of annual primary production. Vollenweider et al. (1974) made this correction by increasing their estimate of annual primary production in western Lake Erie by 10% in order to account for winter primary production. In this study, the sampling season was even shorter, generally including only spring and summer, thus a different correction was required to account for fall and winter production. Given the strong seasonality of primary production in the basin apparent from previous studies (Glooschenko et al. 1974a; Dahl et al. 1995), it was assumed that Spring Primary Production = Fall Primary Production, and Winter Primary Production = ½ Spring Primary Production. The discrepancy between the two approaches, when applied to the 1970 data of Vollenweider et al. (1974) was less than 6%. This was consistent with variability among depth – integrated production models in general (Behrenfeld and Falkowski, 1997) and demonstrated that comparisons among the data sets were feasible.

Primary Production Required (PPR)

PPR, the theoretical amount of primary production required to support the Lake Erie commercial fish catch, was calculated using the model of Pauley and Christensen (1995):

$$PPR = (Catch/9) \times 10^{(TL-1)} \text{ where,}$$

Catch = total catch (fresh weight)

TL = trophic level.

Lake Erie catch data from 1998 (MacGregor, 1999) were inputted into the model and trophic level was assumed to be 4. In practice, however, the trophic level of the commercially important species, e.g. walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), white perch (*Morone Americana*), rainbow smelt (*Osmerus mordax*), white bass (*Morone chrysops*) and lake whitefish (*Coregonus clupeaformis*), ranges from 3.2 to 4.3 (Vander Zanden and Rasmussen, 1996).

Table 1: Mean phytoplankton biovolumes estimated in this study from 2000 and 2001 observations.

Taxon	Genera	Volume (μm^{-3})	N	S.E.
Chlorophyta	*Actinastrum*	1702.7	10	441.0
	Ankistrodesmis	827.7	42	189.2
	Chlamydomonas	259.4	60	12.6
	Chlorella	3.1	1	
	Closteriopsis	224.1	28	35.7
	Coelastrum	83.1	6	23.2
	Crucigenia	2350.0	14	1114.3
	Dictyosphaerium	15208.9	2	12402.7
	Gloeocystis	487.0	31	101.8
	Kirchneriella	15.3	5	3.4
	Micractinium	280.7	8	114.6
	Pediastrum	274317.7	12	153840.1
	Scenedesmes	945.7	44	104.9
	Selenastrum	133.0	24	27.0
	Tetraedron	2064.3	52	430.5
	Volvox	153129.4	4	81002.0
	Westella	1.8	3	4.3
Chrysophyceae	*Ochramonas*	952.9	3	186.3
	Small Chrysophyte	60.2	60	5.0
	Synura	4775.1	22	2078.9
	Tribonema	10840.5	8	7420.1
Cryptophyceae	*Cryptomonas*	1304.7	60	118.9
	Rhodomonas	37.5	60	2.2
Cyanophyta	*Anabaena*	824.9	22	165.4
	Aphanocapsa	3135.8	3	716.7
	Aphanothece	1767.1	1	
	Chrooccocus	338.1	41	93.4
	Coelosphaerium	2412.1	6	722.0
	Holopedium	6159.8	45	1508.0
	Merismopeda	796.6	42	259.0
	Microcystis	66982.4	45	16515.5
	Rhabdoderma	924.8	6	258.5
	Small Blue Green	15.7	25	3.1
Diatomeae	*Asterionella*	7358.4	24	1775.2
	Cyclotella	7009.1	60	1170.4
	Fragillaria	50995.9	20	8129.1
	Melosira	8263.2	46	1539.2
	Navicula	4434.7	29	1275.9
	Stephanodiscus	4331.1	45	684.3
	Synedra	907.5	53	416.2
	Tabellaria	12847.5	4	5217.5
	Thallosaria	7662.2	2	6544.0
Dinophyceae	*Peridinium*	10460.1	38	1833.9
Euglenophyceae	*Trachelemonas*	7250.3	3	1743.7

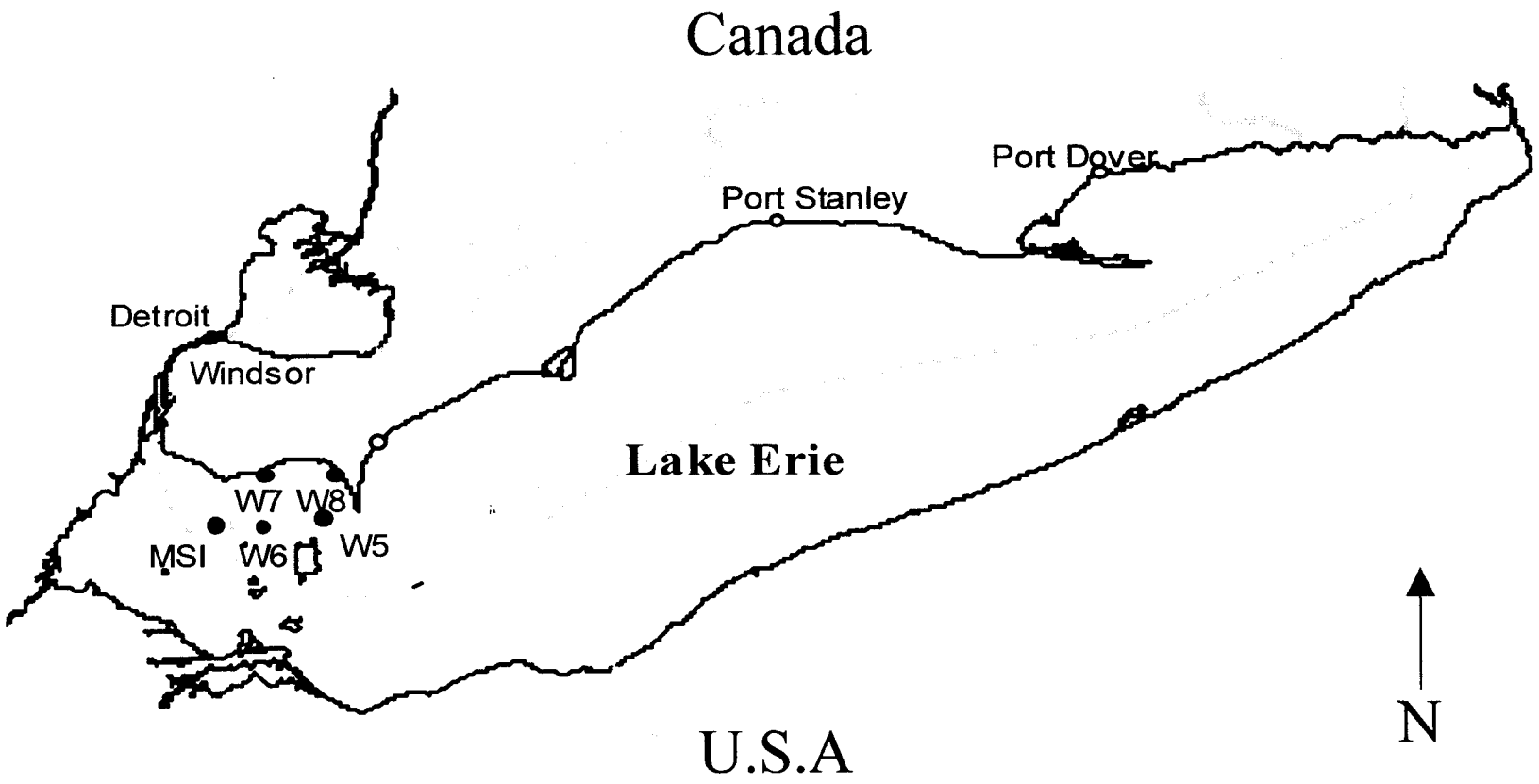


Figure 2: Sampling locations in western Lake Erie

Results

The results of this study will be presented in the order of limnological observations, nutrient levels, phytoplankton biomass and composition, primary productivity and primary production.

Limnology of Western Lake Erie

Temperature

Temperature profiles from MSI are summarized in Figure 3 (a, b and c) for each cruise in 2000, 2001 and 2002. Surface temperatures ranged from 9.9 to 23.4 °C between April and October 2000, 10.1 to 24.3 °C between April and September 2001, and 19.8 to 24.5 °C between June and September 2002. Thermal stratification of the water column was observed on June 26 and October 12, 2000, and on June 13 and June 28, 2002. Otherwise, the water column was well mixed supporting the use of the productivity depth model.

Dissolved oxygen (D.O.)

D.O. concentrations at MSI ranged from 7 to 12 mg l^{-1} between June and October 2000 (Fig. 4a), from 6 to 8 mg l^{-1} between July and September 2001 (Fig. 4b), and from 4 to 9 mg l^{-1} between June and September 2002 (Fig. 4c). Oxygen depletion in the lower water column was observed on June 7 and June 26, 2000 and on June 13 and June 28, 2002.

Specific conductivity

Specific conductivity of the water column at MSI ranged from 0.24 to 0.28 mS cm^{-1} between June and October 2000 (Fig. 5a), from 0.24 to 0.26 mS cm^{-1} between July and September 2001 (Fig. 5b), and from 0.23 to 0.26 mS cm^{-1} between June and September 2002 (Fig. 5c).

Reduction potential (redox)

Reduction potential at MSI ranged from 168 to 330 mV between June and October 2000 (Fig. 6a), from 220 to 315 mV between July and September 2001 (Fig. 6b), and from 94 to 300 mV between June and September 2002 (Fig. 6c). Water column fluctuations in redox were observed on June 26 and August 4, 2000 and on July 12 and July 24, 2002.

pH

pH values at MSI ranged from 8.2 to 8.4 during the study period.

Vertical attenuation coefficient (ϵ_{par})

ϵ_{par} measurements for 2000, 2001 and 2002 are summarized in Figure 7 (a and b). In 2000, ϵ_{par} ranged from 0.34 to 2.28 m^{-1} at W5 between May and November, from 0.39 to 2.51 m^{-1} at W8 during the same period, and from 0.47 to 0.67 m^{-1} between April and August, at MSI. In 2001, ϵ_{par} ranged from 0.14 to 0.72 m^{-1} at W5 during May to early October, from 0.27 to 4.23 m^{-1} at W8 between May and late October and from 0.42 to 0.77 m^{-1} at MSI between June and September. Finally, in 2002, ϵ_{par} ranged from 0.29 to 1.06 m^{-1} at MSI between June and September.

Euphotic depth (Z_{eu})

Euphotic depth at sites W5 and W8 ranged from 1.7 to 10 metres in 2000 and from 1.2 to 10 m in 2001. At MSI, Z_{eu} ranged from 2.8 to 10 metres in 2000, 5.4 to 9.2 metres during 2001 and from 4.4 to 10 metres in 2002. Z_{eu} is summarized in Figure 8 (a and b).

Nutrients

Total phosphorus

Mean total phosphorus concentrations from 2000 to 2002 are summarized in Figure 9. In 2000, total phosphorus levels ranged from 0.01 to 0.04 mg l^{-1} at W5 and W8. 2001 concentrations ranged from 0.01 to 0.1 mg l^{-1} at W5, W6, W7 and W8, and from 0.01 to 0.03 at MSI. 2002 levels at MSI ranged from 0.03 to 0.07 mg l^{-1}.

A comparison of results for total phosphorus samples processed by the Ontario Ministry of Natural Resources (MNR) and by the Great Lakes Institute for Environmental Research (GLIER) for 2001, sites W5 and W8, are shown in Figure 10. Mean spring TP concentrations of 0.017 mg l^{-1} +/- 0.0024 (MNR) and 0.017 mg l^{-1} +/- 0.0032 (GLIER) showed no significant difference ($P > 0.05$). Similarly, mean summer TP concentrations of 0.026 mg l^{-1} +/- 0.0016 (MNR) and 0.023 mg l^{-1} +/- 0.0032 (GLIER) showed no significant difference ($P > 0.05$). Finally mean annual TP concentrations of 0.022 mg l^{-1} +/- 0.0017 (MNR) and 0.019 mg l^{-1} +/- 0.0022 (GLIER) showed no significant difference ($P > 0.05$).

Nitrate

Mean nitrate concentrations are shown in Figure 11. In 2000, concentrations ranged from 0.04 to 0.5 mg l^{-1} at W5, W6, W7 and W8 and from 0.05 to 0.4 mg l^{-1} at MSI. 2001 concentrations ranged from 0.08 to 0.6 mg l^{-1} at W5, W6, W7 and W8, and from 0.2 to 0.6 mg l^{-1} at MSI. 2002 concentrations ranged from 0.1 to 0.5 mg l^{-1} at MSI. A strong seasonal pattern was apparent in nitrate levels throughout the study, which tended to peak in the spring and trough in late summer or early fall.

Algal standing crop

Chlorophyll a

Mean chlorophyll a concentrations from sites W5, W6, W7, and W8 ranged from 3.7 to 8.0 mg m^{-3} in 2000, and from 1.8 to 13.0 mg m^{-3} in 2001. At MSI, water column mean chlorophyll a concentrations ranged from 0.7 to 9.1 mg m^{-3} in 2002. Results are summarized in Figure 12.

Phytoplankton biomass and composition

Average water column phytoplankton biomass and percent community composition at MSI are shown in Figure 13. Fresh weight biomass ranged from 2.9 to 12.1 g m^{-3} in 2000 (Fig. 13a) and from 3.5 to 5.3 g m^{-3} in 2001 (Fig. 13b). In 2000, Chlorophyta represented 9 to 27 % of the biomass, Chrysophyceae: 0.1 to 2 %, Cryptophyceae: 5 to 45 %, Cyanophyta: 2 to 19 %, Diatomeae: 30 to 78%, Dinophyceae: 0 to 4% and Euglenophyceae less than 1 % (Fig. 13a). Similarly, in 2001 composition of the phytoplankton community by biomass was represented by Chlorophyta: 10 to 38 %,

Chrysophyceae: 6 to 16 %, Cyanophyceae: 10 to 35 %, Diatomeae: 32 to 52 %, Dinophyceae: 0.6 to 6 % and Euglenophyceae less than 1 % (Fig. 13b).

The seasonal distribution of phytoplankton composition at MSI is shown in Figure 14. In spring 2000, the taxa contributing the most to biomass were: Diatomeae (56%), Cryptophyceae (23%), Chlorophyta (13.2%), and Cyanophyta (5.4%). In spring 2001, the dominant taxa were: Diatomeae (42.6%), Chlorophyta (29.9%), Cyanophyta (15.2%) and Cryptophyceae (7.7%). Summer 2000 was composed of Diatomeae (42.7%), Chlorophyta (21.6%), Cryptophyceae (16.1%) and Cyanophyta (15.4%). Summer 2001 was composed of Diatomeae (42%), Cryptophyceae (12.8%), Chlorophyta (27.3%) and Cyanophyta (12.5%). Fall 2000 composition was Diatomeae (78%), Chlorophyta (13.4%) and Cyanophyta (5.5%).

Common phytoplankton genera at MSI for 2000 and 2001 are shown in Tables 2 and 3. The most common genera, by weight, in spring 2000 were the diatoms *Cyclotella* and *Melosira*, and the cryptophyte *Cryptomonas*. In spring 2001, the most common genera were the diatoms *Cyclotella* and *Fragillaria* and the cyanophyte *Microcystis*. In summer 2000, the diatoms *Cyclotella*, *Fragillaria* and *Stephanodiscus* and the cryptophyte *Cryptomonas* were most prevalent. Summer 2001 was composed of the diatoms *Cyclotella* and *Melosira* and the chlorophyte *Pediastrum*. The diatom *Melosira* was the most commonly occurring genus in Fall 2000.

Primary productivity

Size fractionated productivity (SFP)

Mean rates of primary productivity at sites W5, W6, W7 and W8 for each size fraction per cruise are summarized in Figures 15a and 15b. In 2000, the largest size fraction, >20 μm, had no measurable growth during the spring, ranged from 2.9 to 19.7 mg C m^{-3} h^{-1} during the summer, and from 0.2 to 13.2 mg C m^{-3} h^{-1} in the fall. The 2 - 20 μm fraction was the most productive size class on all cruises at 0.7 mg C m^{-3} h^{-1} in the spring; from 17.1 to 51.3 mg C m^{-3} h^{-1} in the summer, and from 3.2 to 25.8 mg C m^{-3} h^{-1} in the fall. Finally, the <2 μm size fraction productivity rates were 2.0 mg C m^{-3} h^{-1} in the spring; 1.4 to 2.7 mg C m^{-3} h^{-1} in the summer, and 0.02 to 4.05 mg C m^{-3} h^{-1} in the fall.

In 2001, primary productivity in the >20 μm category ranged from 0.5 to 0.7 mg C m^{-3} h^{-1} in the spring; 0.1 to 7.1 mg C m^{-3} h^{-1} in the summer and 0.8 to 8.3 mg C m^{-3} h^{-1} in the fall. As in 2000, the 2-20 μm fraction was most productive and ranged from 4.1 to 5.3 mg C m^{-3} h^{-1} in spring, 15.7 to 28.9 mg C m^{-3} h^{-1} in summer and 7.6 to 17.4 mg C m^{-3} h^{-1} in fall. Primary productivity in the <2 μm fraction ranged from 0.6 to 2.7 mg C m^{-3} h^{-1} in the spring; 2.8 to 5.2 mg C m^{-3} h^{-1} in the summer and 0.3 to 3.1 mg C m^{-3} h^{-1} in the fall.

Light and dark bottles (LDB)

Water column mean productivity rates at MSI for 2001 and 2002 are illustrated in Figures 16a and 16b. Productivity rates in 2001 ranged from 3.8 to 17.0 mg C m^{-3} h^{-1} in the spring and from 22.5 to 42.5 mg C m^{-3} h^{-1} in the summer. In 2002, productivity rates

ranged from 7.6 to 9.5 mg C m^{-3} h^{-1} in the late spring and from 11.8 to 34.0 mg C m^{-3} h^{-1} in the summer.

Comparison of techniques

Both SFP and LDB techniques were deployed throughout the summer of 2001. Mean water column productivity rates for spring and summer of 2001 are compared in Figure 17. Spring mean primary productivity was 7.2 mg C m^{-3} h^{-1} +/- 0.27 (SFP) and 10.7 mg C m^{-3} h^{-1} +/- 3.8 (LDB). Summer mean productivity was 29.8 mg C m^{-3} h^{-1} +/- 2.7 (SFP) and 30.6 mg C m^{-3} h^{-1} +/- 4.4 (LDB). No significant differences in carbon uptake were apparent ($P > 0.05$).

Primary production

Average daily rates of areal primary production are summarized in Figure 18. At sites W5, W6, W7 and W8, daily average primary production ranged from 0.6 to 4.2 g C m^{-2} d^{-1} in 2000 (Fig. 18a) and from 0.8 to 3.2 g C m^{-2} d^{-1} in 2001 (Fig. 18b). At MSI, primary production ranged from 0.3 to 2.3 g C m^{-2} d^{-1} in 2001 (Fig. 18c) and from 0.8 to 2.1 in g C m^{-2} d^{-1} in 2002 (Fig. 18d).

Figure 19 compares average daily primary production rates for all stations in 2001 derived from SFP and LDB techniques. Mean spring production was 0.6 g C m^{-2} d^{-1} +/- 0.16 (SFP) and 0.8 g C m^{-2} d^{-1} +/- 0.40 (LDB). Mean summer production was 2.2 g C m^{-2} d^{-1} +/- 0.32 (SFP) and 2.0 g C m^{-2} d^{-1} +/- 0.16. These results indicate that there was good agreement between the two sampling regimes and methodologies in 2001.

Annual primary production was calculated to be 372 g C m^{-2} y^{-1} in 2000, 351 g C m^{-2} y^{-1} in 2001 using the SFP techniques, 350 g C m^{-2} y^{-1} in 2001 and 325 g C m^{-2} y^{-1} in 2002 using the LDB method.

Carbon turnover and carbon assimilation

Western basin mean carbon turnover times in the June to September period were 2.3 d +/- 1.2 in 2000, 2.2 d +/- 0.3 in 2001 and 1.7 d +/- 0.7 in 2002. Mean carbon assimilation rates in the same period were 39.3 mg C mg Chl $\underline{a}^{-1}$ d^{-1} +/- 25.2 in 2000, 21.0 mg C mg Chl $\underline{a}^{-1}$ d^{-1} +/- 3.4 in 2001, and 54.9 mg C mg Chl $\underline{a}^{-1}$ d^{-1} +/- 15.5 in 2002.

Primary production required (PPR)

The primary production required to sustain the 1998 catch of 17.8 million kg fresh weight (MacGregor, 1999) for all three basins of Lake Erie was 1 976.9 kt C y^{-1} assuming a trophic level of 4. Two estimates of primary production available (PPA) were made. PPA(1) was determined to be 8 460.2 kt C y^{-1} by applying west basin annual primary production rates lake wide. Annual primary production of 334 g C m^{-2} y^{-1} was applied to Lake Erie's surface area of 25 320 km^{-2} (Schertzer, 1999). Annual primary production was the mean of 1970 (Vollenweider et al, 1974), 1993 (Dahl et al. 1993), 2000, 2001 and 2002. PPR was therefore 23.3% of PPA(1). PPA(2) was determined to be 5 834.3 kt C y^{-1} based on 1970 primary production data for the west, central and eastern basins (Vollenweider et al. 1974). The surface areas for the three respective basins were 2 912 km^{-2}, 16 746 km^{-2} and 5 672 km^{-2} (Schertzer, 1999). PPR was then 33.9% of PPA(2). These results are summarized in Figure 20.

Table 2: Dominant phytoplankton genera (greater than 5% biomass) in 2000.

Cruise	Taxon	Genus	% Biomass
April 28	Chlorophyta	Chlamydomonas	11.4
		Tetraedron	7.7
	Cryptophyceae	Cryptomonas	6.9
	Cyanophyta	Coelospaerium	5.1
	Diatomeae	Cyclotella	22.3
		Fragillaria	27.1
		Navicula	7.1
June 7	Chlorophyta	Chlamydomonas	9.5
		Tetraedron	5.4
	Cryptophyceae	Cryptomonas	13.6
	Cyanophyta	Merismopeda	6.4
	Diatomeae	Cyclotella	10.3
		Melosira	34.4
June 26	Chlorophyta	Chlamydomonas	6.1
	Cryptophyceae	Cryptomonas	23.8
	Diatomeae	Cyclotella	26.5
		Fragillaria	5.4
		Melosira	14.7
		Stephanodiscus	10.4
July 7	Chlorophyta	Chlamydomonas	8.4
	Cryptophyceae	Cryptomonas	7.3
	Cyanophyta	Holopedium	7.9
		Microcystis	6.0
	Diatomeae	Cyclotella	22.8
		Melosira	14.6
		Stephanodiscus	7.5
July 24	Chlorophyta	Chlamydomonas	8.1
	Cryptophyceae	Cryptomonas	47.1
	Bacillariophyceae	Asterionella	8.9
		Cyclotella	5.8
		Fragillaria	5.9
August 4	Chlorophyta	Pediastrum	11.9
	Cryptophyceae	Cryptomonas	5.8
	Cyanophyta	Microcystis	10.9
	Diatomeae	Cyclotella	10.2
		Fragillaria	34.6
	Dinophyceae	Peridinium	6.1
August 24	Chlorophyta	Chlamydomonas	6.1
		Pediastrum	10.9
	Cryptophyceae	Cryptomonas	12.0
	Cyanophyta	Microcystis	7.3
	Diatomeae	Cyclotella	17.3
		Melosira	7.9
		Stephanodiscus	18.8
October 12	Chlorophyta	Pediastrum	7.1
	Diatomeae	Melosira	77.5

Table 3: Dominant phytoplankton genera (greater than 5% biomass) in 2001.

Cruise	Taxon	Genus	% Biomass
April 27	Chlorophyta	Chlamydomonas	8.8
		Volvox	7.4
	Cyanophyta	Microcystis	10.3
	Diatomeae	Cyclotella	21.9
		Fragillaria	18.7
May 29	Chlorophyta	Chlamydomonas	7.5
	Cyanophyta	Microcystis	22.6
	Diatomeae	Cyclotella	11.8
		Melosira	16.8
	Dinophyceae	Peridinium	10.6
June 23	Chlorophyta	Chlamydomonas	12.1
		Pediastrum	14.3
	Cryptophyceae	Cryptomonas	7.2
	Cyanophyta	Microcystis	8.1
	Diatomeae	Cyclotella	32.9
		Stephanodiscus	5.7
July 13	Chlorophyta	Chlamydomonas	10.2
		Pediastrum	9.2
		Volvox	7.5
	Cryptophyceae	Cryptomonas	9.7
	Cyanophyta	Holopedium	5.9
	Diatomeae	Cyclotella	21.5
		Fragillaria	15.1
	Dinophyceae	Peridinium	5.3
July 30	Chlorophyta	Chlamydomonas	9.7
		Pediastrum	20.8
	Cryptophyceae	Cryptomonas	12.9
	Cyanophyta	Microcystis	8.1
	Diatomeae	Cyclotella	17.7
		Fragillaria	12.7
August 24	Chlorophyta	Chlamydomonas	6.8
		Volvox	7.7
	Cryptophyceae	Cryptomonas	10.3
	Diatomeae	Cyclotella	20.0
		Melosira	30.1
September 6	Chlorophyta	Chlamydomonas	9.2
	Cryptophyceae	Cryptomonas	16.4
	Cyanophyta	Microcystis	7.8
	Diatomeae	Cyclotella	28.4
		Melosira	7.2
		Stephanodiscus	11.1

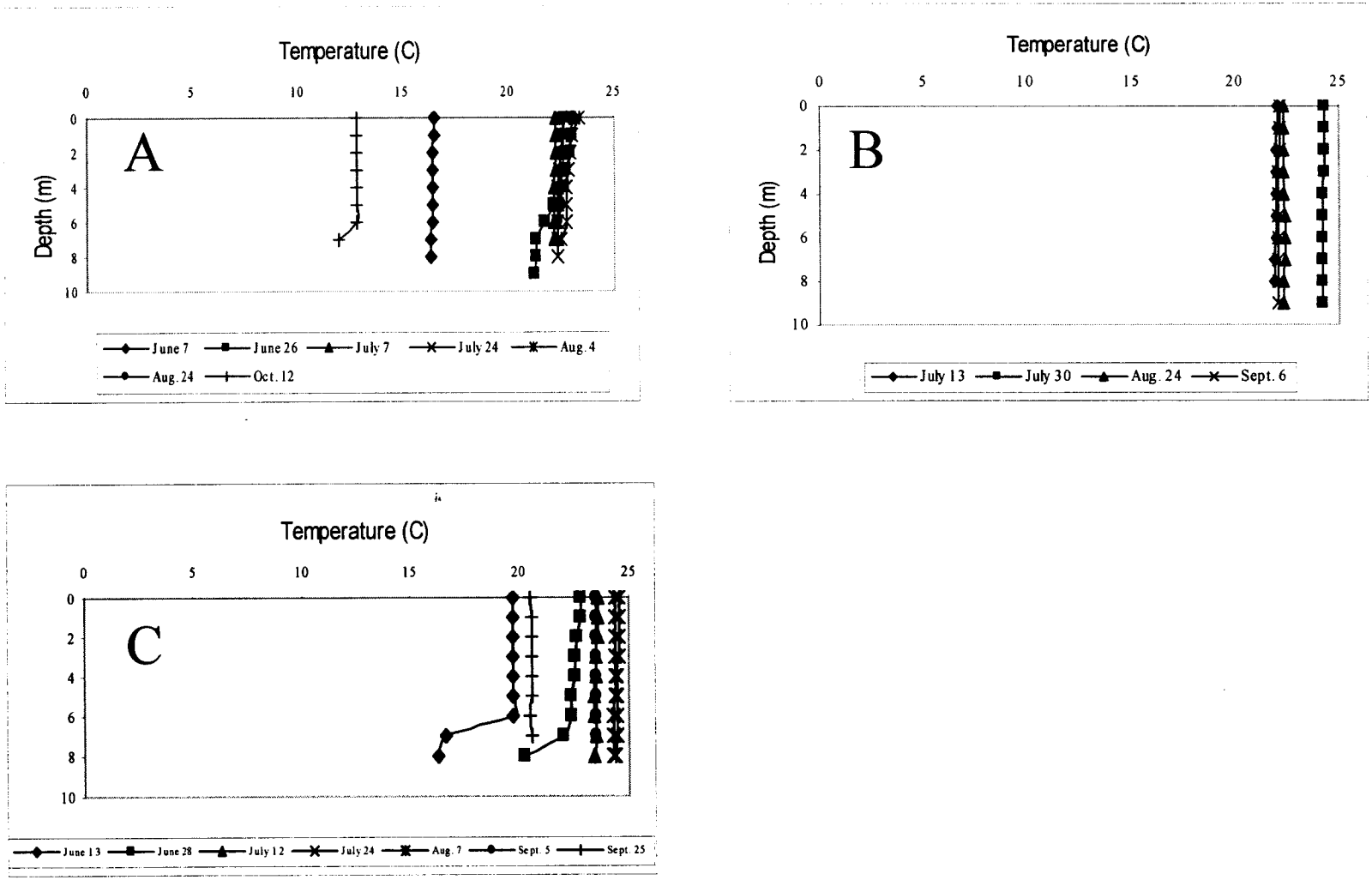


Figure 3: Temperature (^{0}C) profiles at MSI for A: 2000; B: 2001 and C: 2002

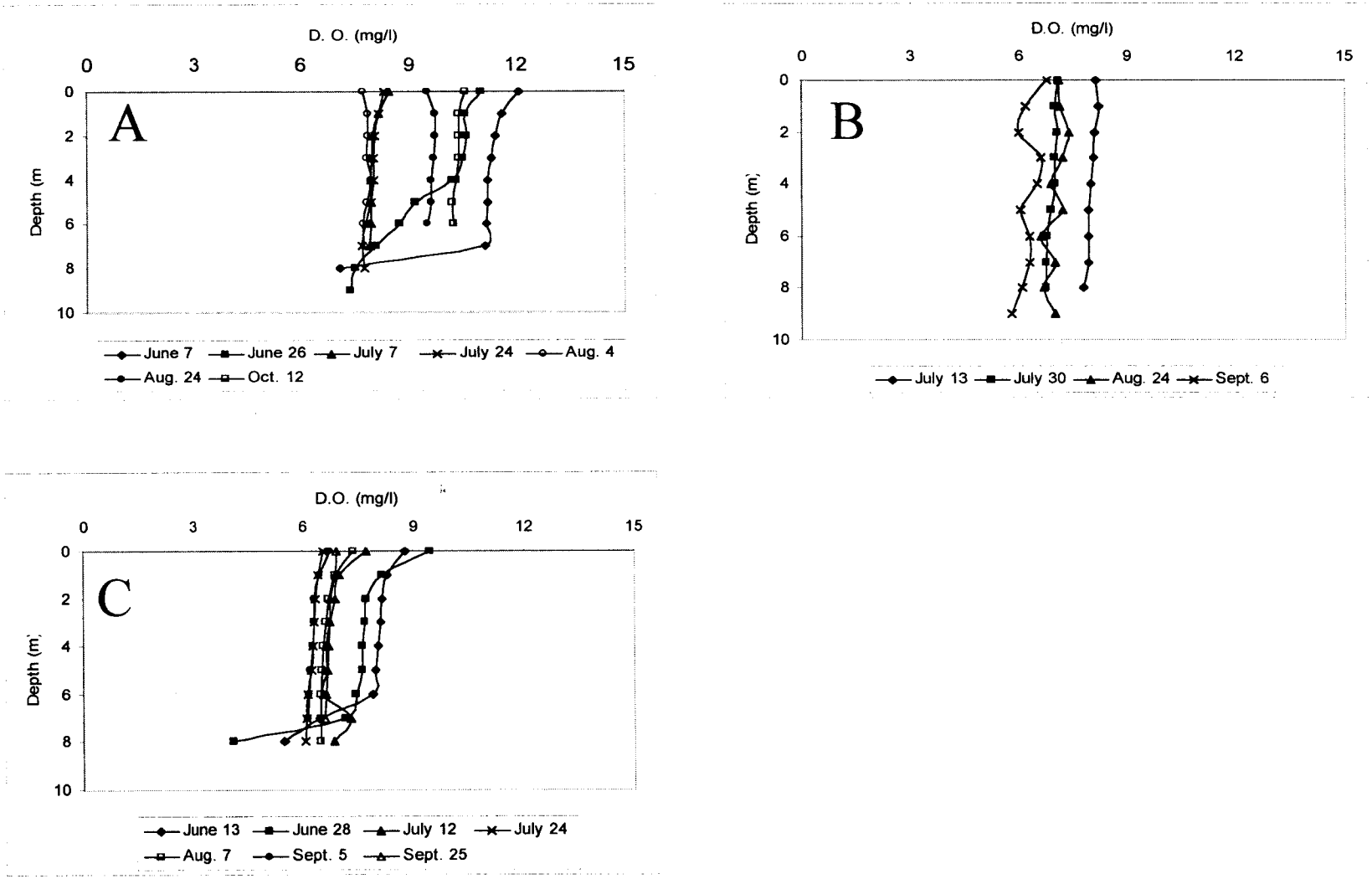
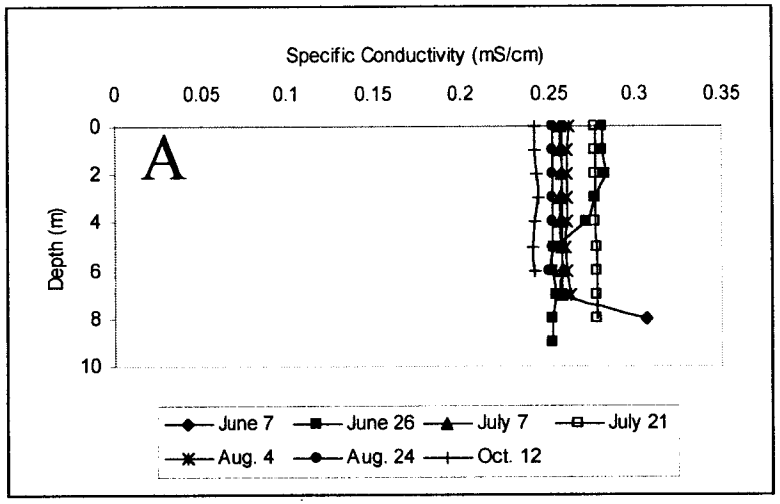
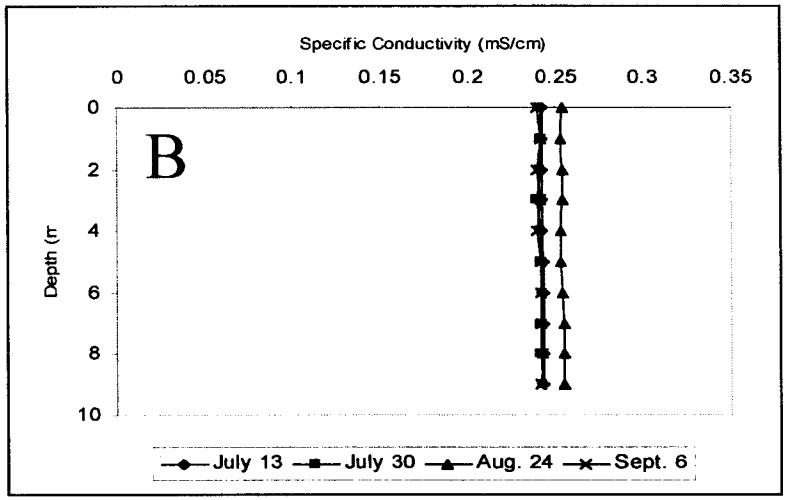


Figure 4: Dissolved Oxygen (mg l^{-1}) profiles at MSI for A: 2000, B: 2001 and C: 2002.





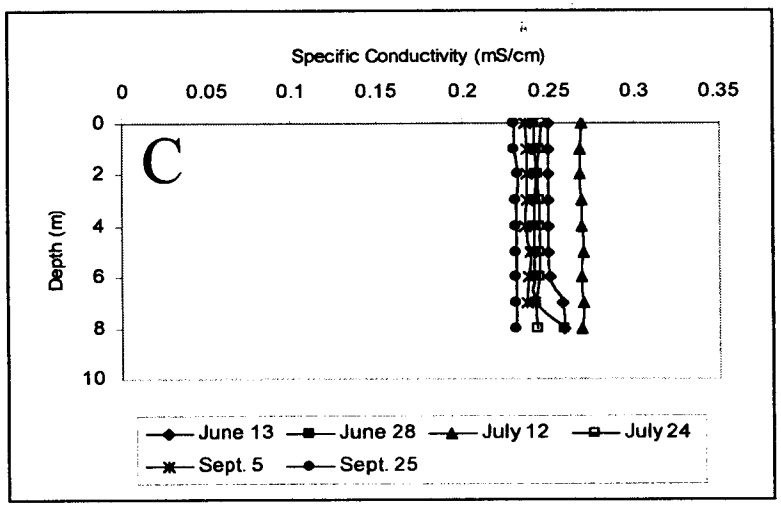
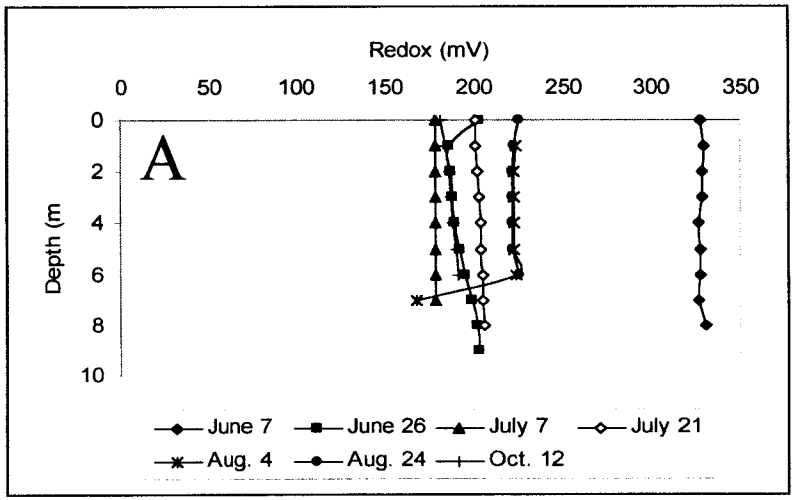
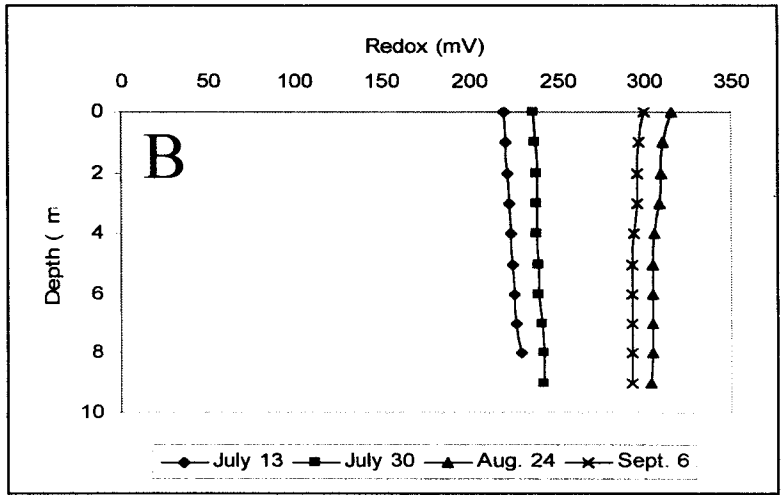


Figure 5: Specific Conductivity (mS/cm) profiles at MSI for A: 2000, B: 2001, and C: 2002





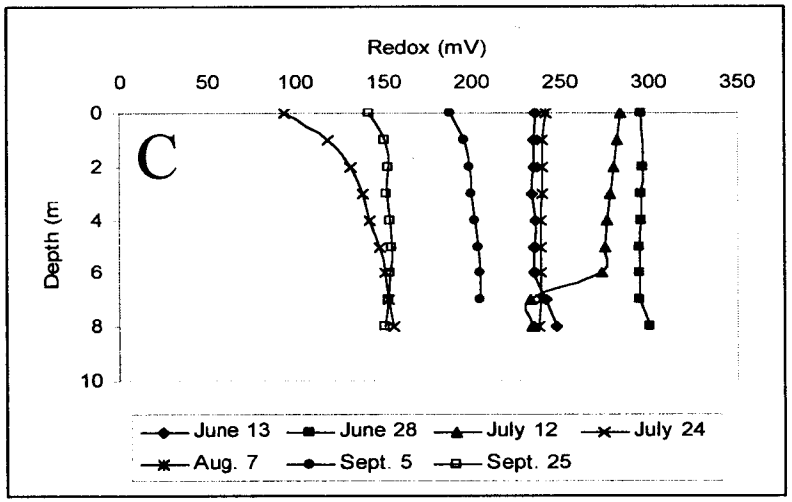


Figure 6: Reduction Potential Profiles (mV) at MSI for A: 2000, B: 2001 and C: 2002

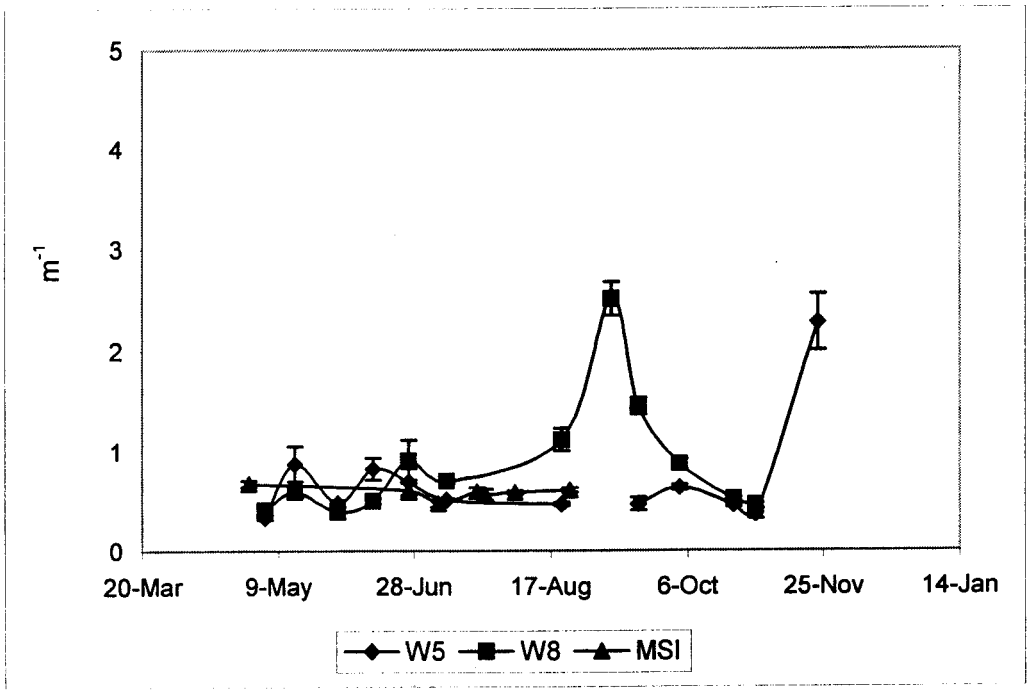


Figure 7a: The mean (+/- 1 S.E.) vertical attenuation coefficient, ε_{par} (m^{-1}), calculated for all cruises in 2000.

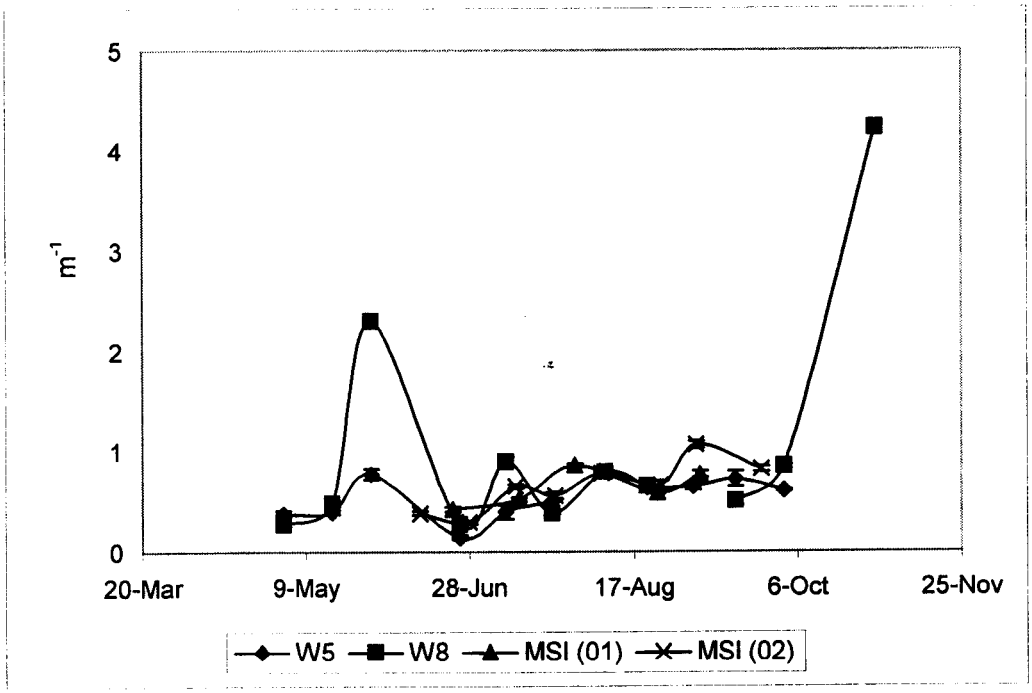


Figure 7b: The mean (+/- 1 S.E.) vertical attenuation coefficient, ε_{par} (m^{-1}) calculated for all cruises in 2001 and 2002.

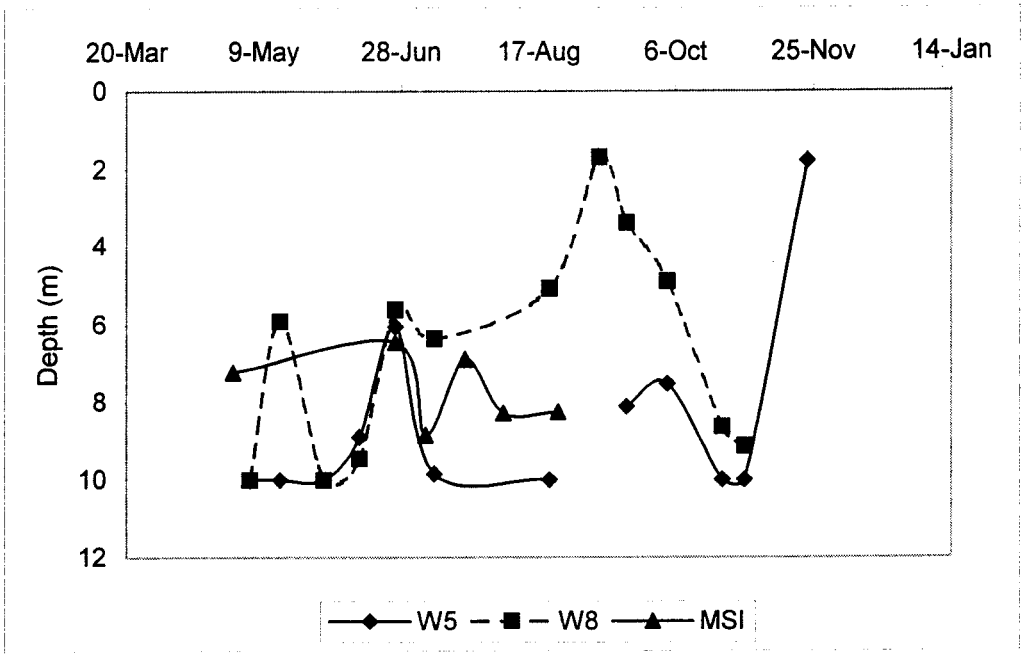


Figure 8a: Eupthotic depth, Z_{eu} (m), at W5, W8 and MSI for 2000.

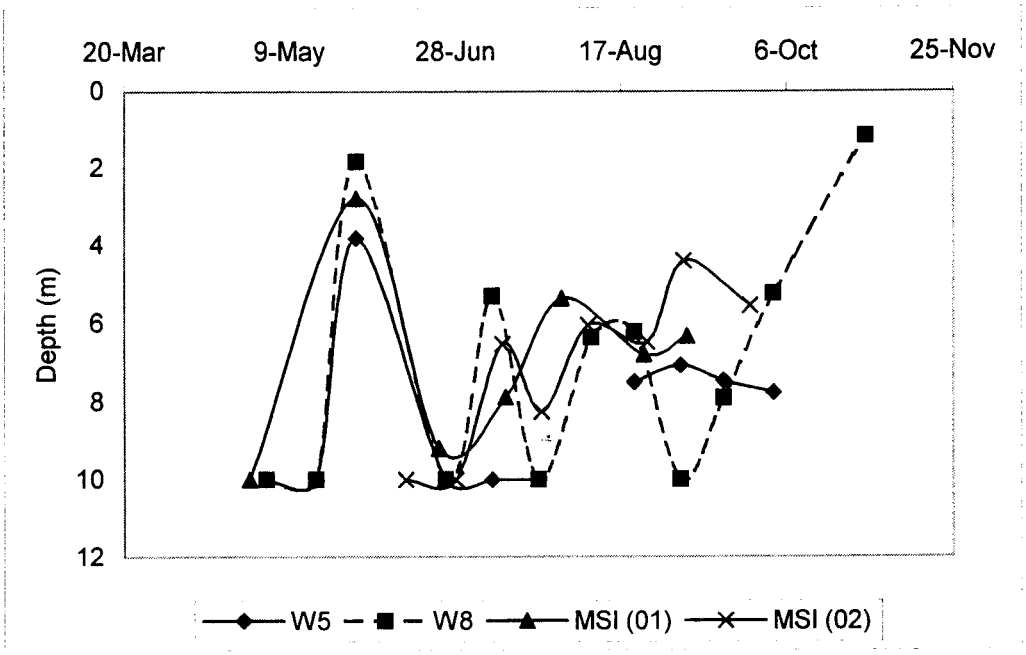


Figure 8b: Euphotic depth, Z_{eu} (m), at W5, W8 and MSI for 2001 and 2002.

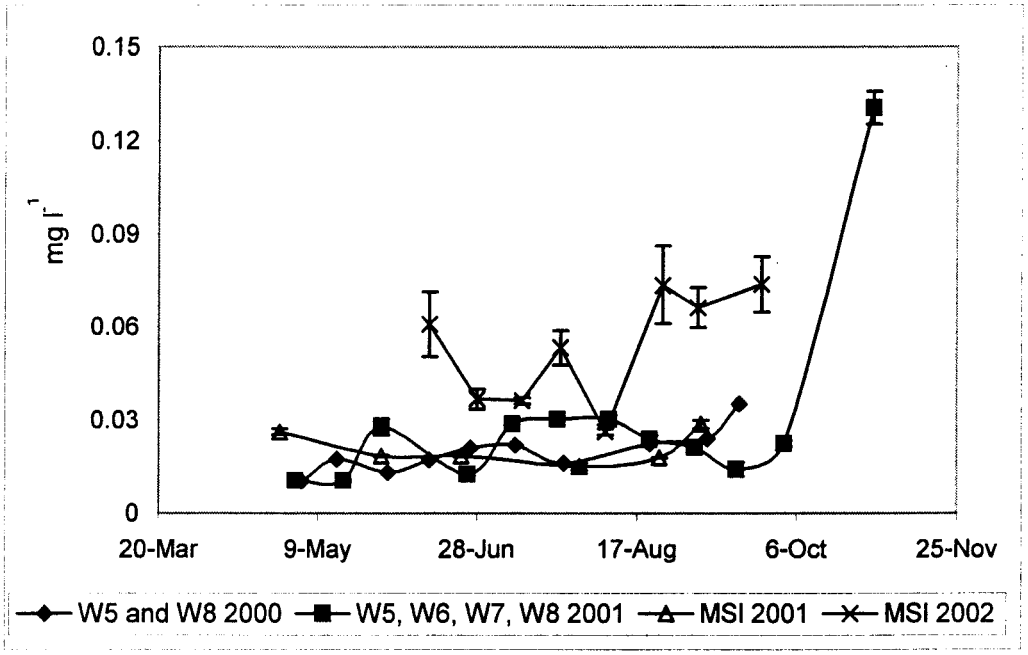


Figure 9: Mean (+/- 1 S.E.) total phosphorus (TP) concentrations (mg l^{-1}) for 2000 (W5, W8), 2001 (W5, W6, W7, W8, MSI) and 2002 (MSI).

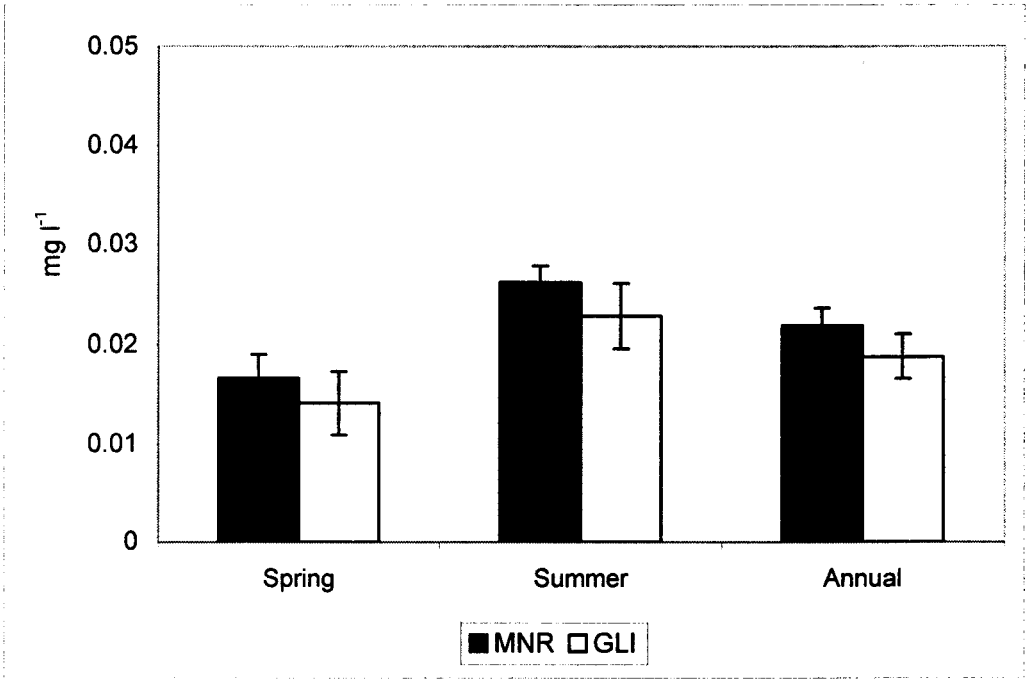


Figure 10: Seasonal mean (+/- 1 S.E.) total phosphorus (TP) concentrations (mg l^{-1}) from the Ministry of Natural Resources (MNR) and the Great Lakes Institute for Environmental Research (GLI). Results are from sites W5 and W8, May to September 2001.

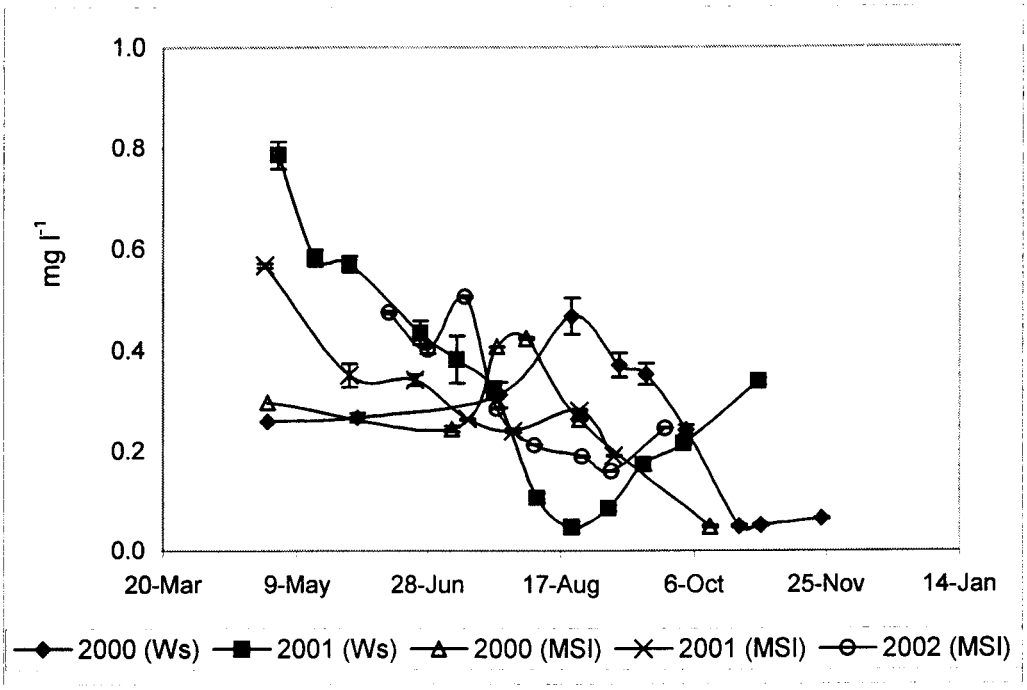


Figure 11: Mean (+/- 1 S.E.) nitrate concentrations (mg l^{-1}) at all sites in 2000, 2001 and 2002.

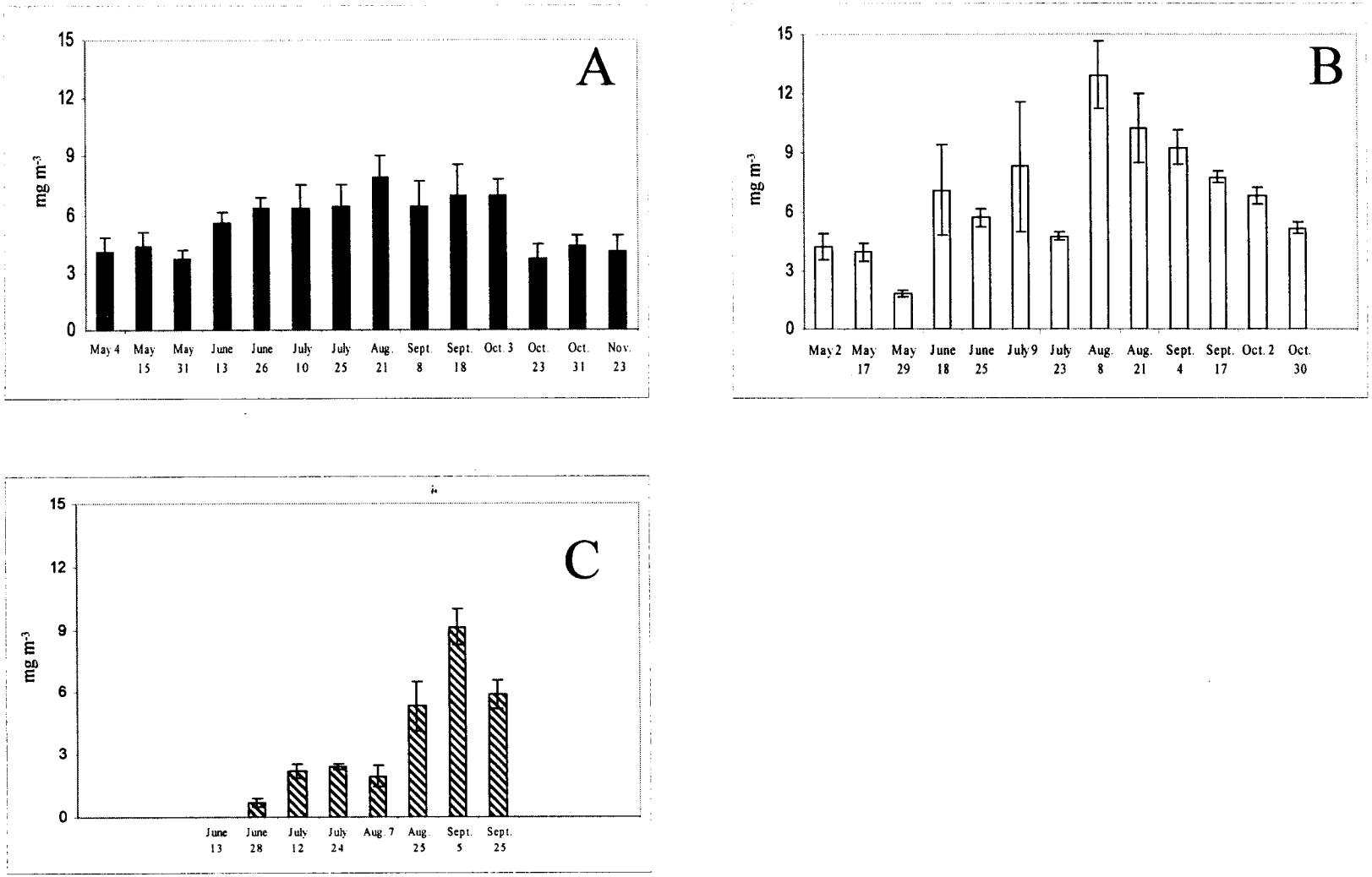


Figure 12: Mean (+/- 1 S.E.) chlorophyll a concentrations (mg m^{-3}) for A: 2000 (W5, W6, W7, W8); B: 2001 (W5, W6, W7, W8); C: 2002 (MSI).

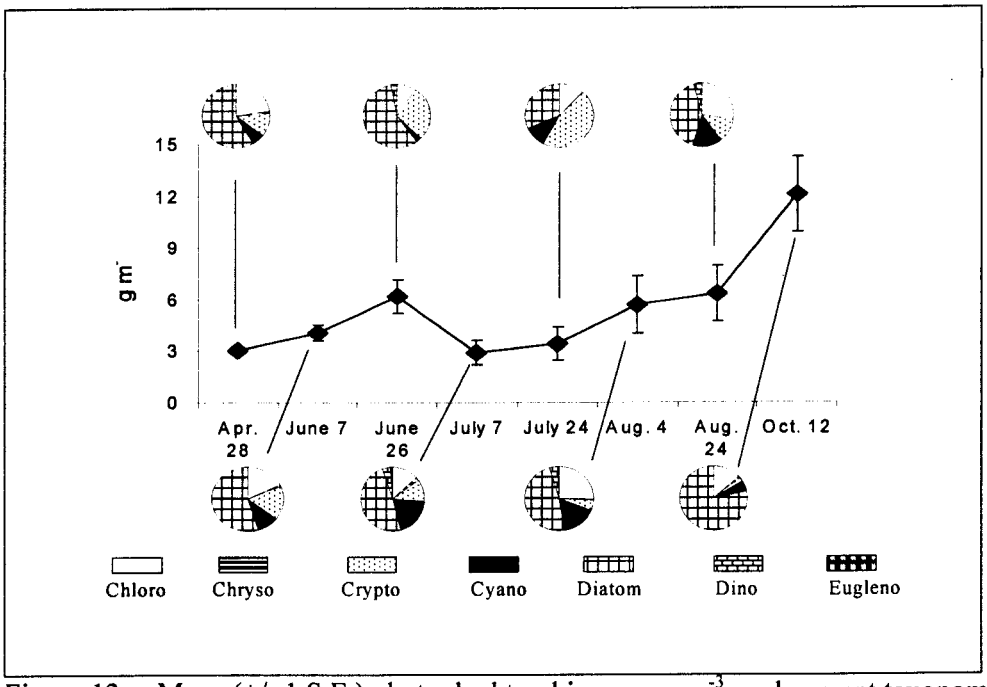


Figure 13a: Mean (+/- 1 S.E.) phytoplankton biomass, g m^{-3}, and percent taxonomic composition by weight for each cruise in 2000. Chlor = Chlorphyta, Chryso = Chrysophyceae, Crypto = Cryprophyceae, Cyano = Cyanophyta Diatom = Diatomeae, Dino = Dinophyceae and Eugleno = Euglenophyceae.

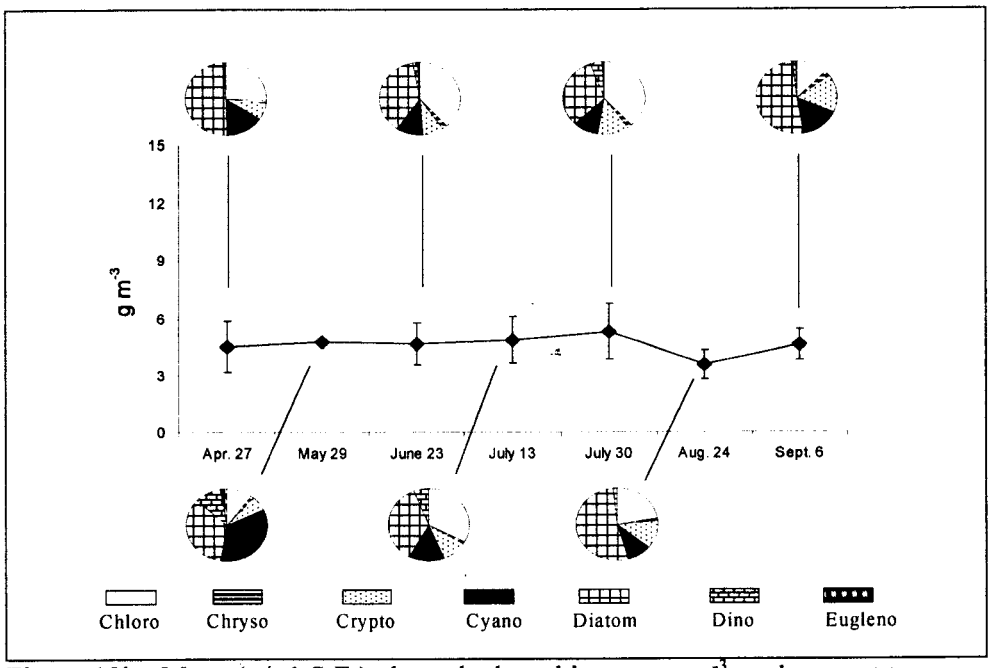


Figure 13b: Mean (+/- 1 S.E.) phytoplankton biomass, g m^{-3}, and percent taxonomic composition by weight for each cruise in 2001. Chlor = Chlorphyta, Chryso = Chrysophyceae, Crypto = Cryprophyceae, Cyano = Cyanophyta Diatom = Diatomeae, Dino = Dinophyceae and Eugleno = Euglenophyceae.

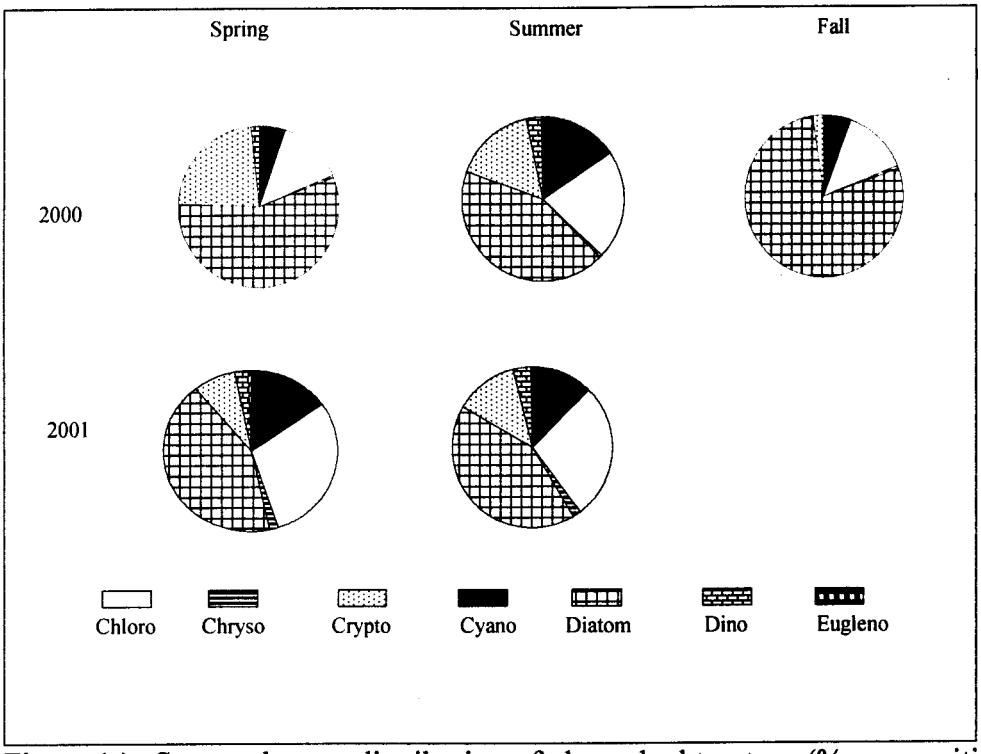


Figure 14: Seasonal mean distribution of phytoplankton taxa (% composition by biomass) in 2000 and 2001. Chlor = Chlorphyta, Chryso = Chrysophyceae, Crypto = Cryprophyceae, Cyano = Cyanophyta Diatom = Diatomeae, Dino = Dinophyceae and Eugleno = Euglenophyceae.

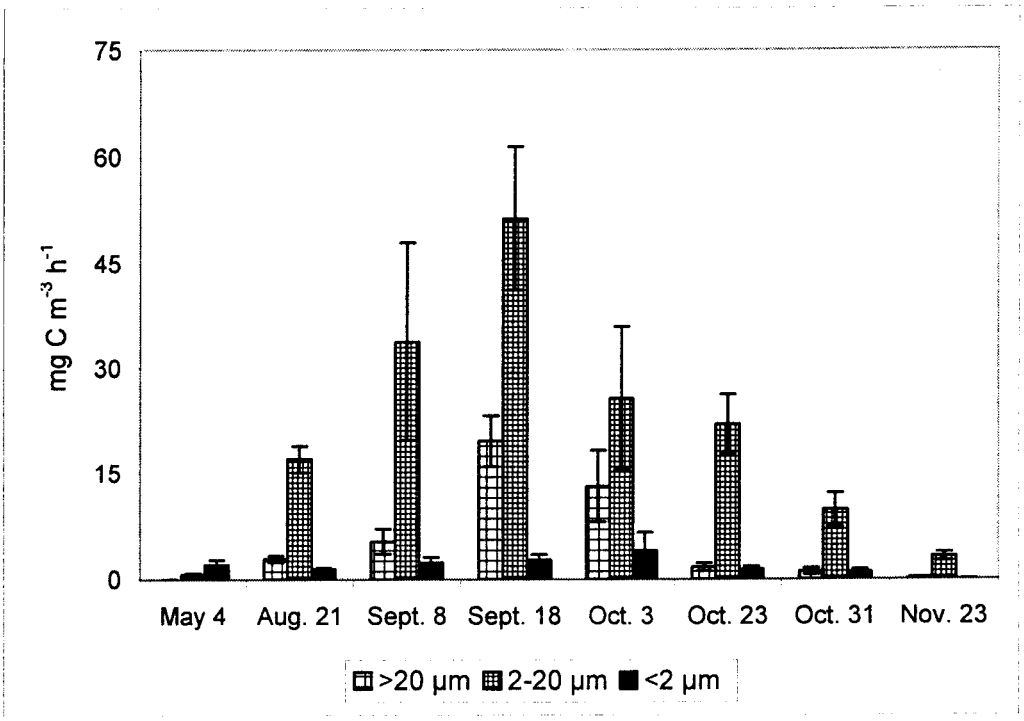


Figure 15a: Mean (+/- 1 S.E.) size fractionated primary productivity (SFP), mg C m^{-3} h^{-1}, for 2000 at sites W5, W6, W7 and W8.

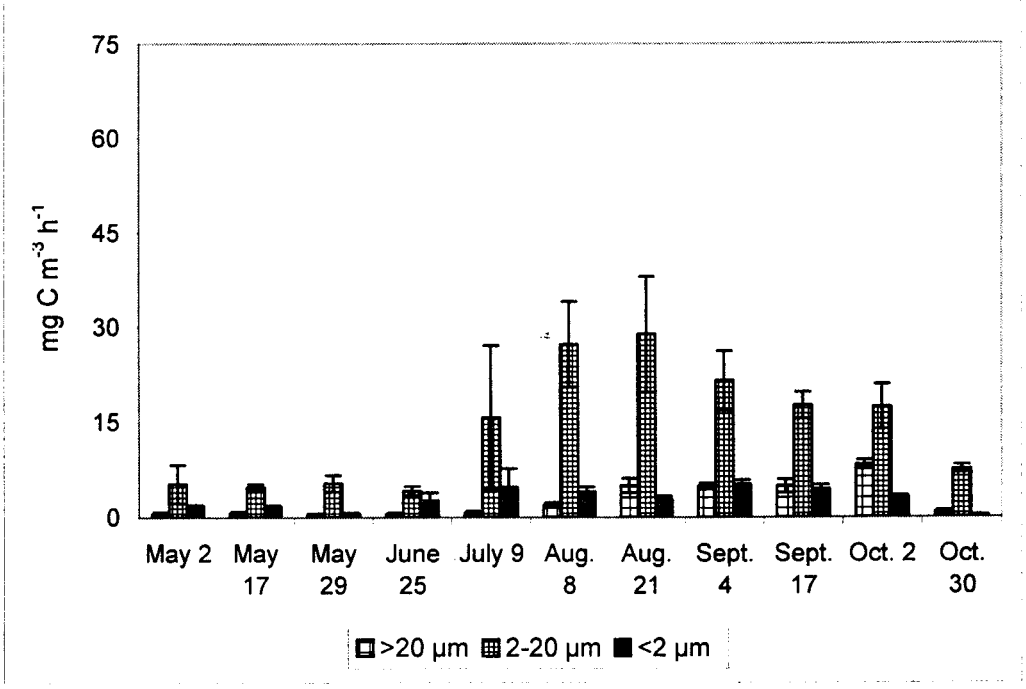


Figure 15b: Mean (+/- 1 S.E.) size fractionated primary productivity (SFP), mg C m^{-3} h^{-1}, for 2001 at sites W5, W6, W7 and W8.

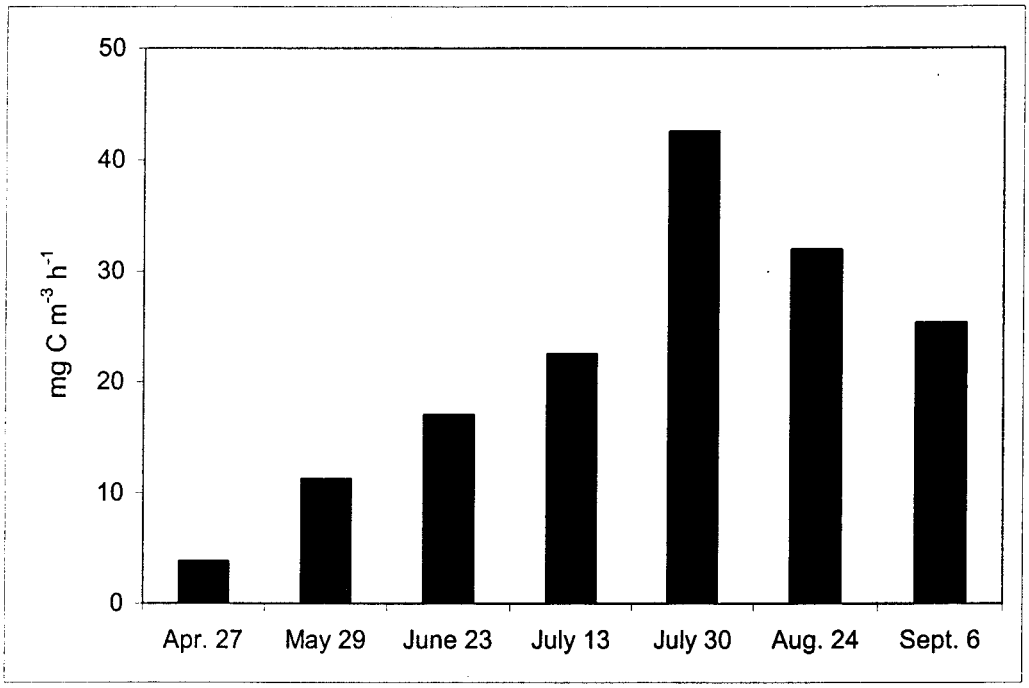


Figure 16a: Weighted mean water column primary productivity, mg C m^{-3} h^{-1}, at MSI (LDB) for 2001.

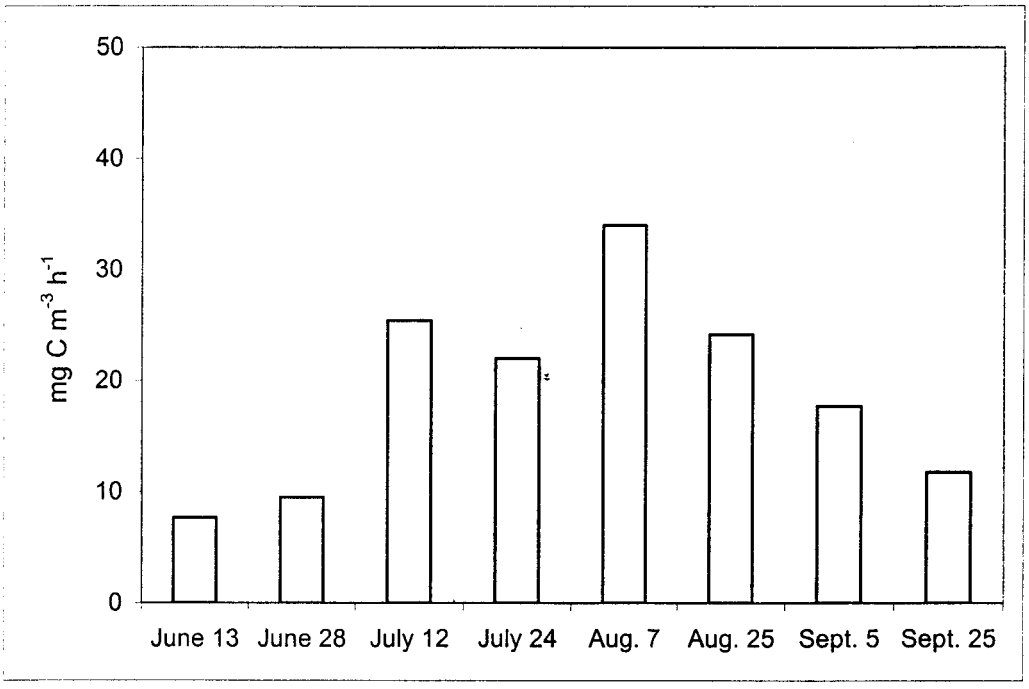


Figure 16b: Weighted mean water column primary productivity, mg C m^{-3} h^{-1}, at MSI (LDB) for 2002.

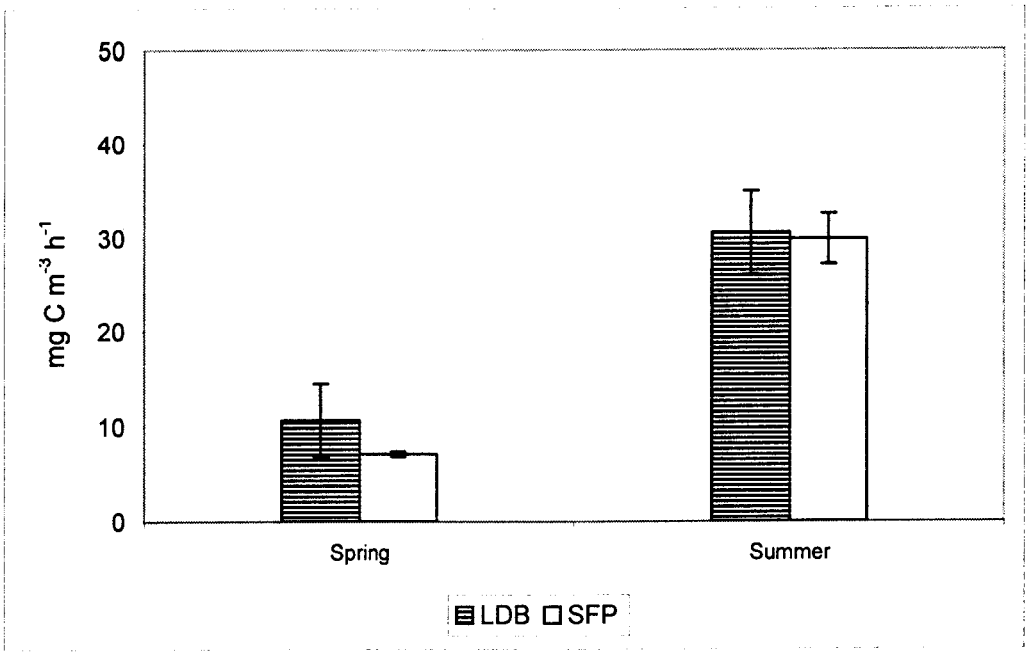


Figure 17: Seasonal mean (+/- 1 S.E.) rates of primary productivity, mg C m^{-3} h^{-1}, estimated from SFP and LDB techniques during 2001.

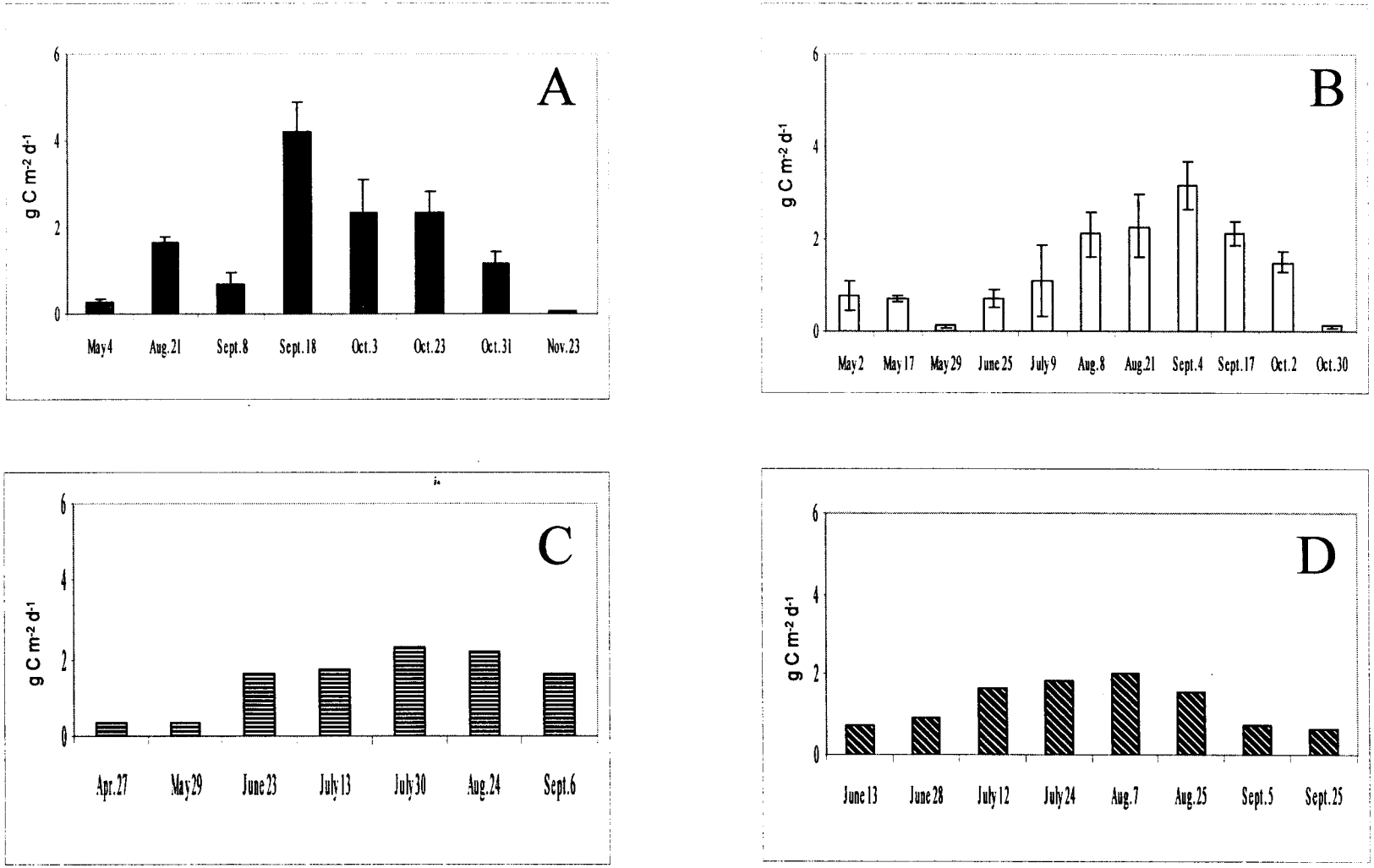


Figure 18: Daily primary production, g C m^{-2} d^{-1}, in western Lake Erie for A: 2000 (W5, W6, W7, W8, +/- 1 S.E.); B: 2001 (W5, W6, W7, W8, +/- 1 S.E.); C: 2001 (MSI) and D: 2002 (MSI).

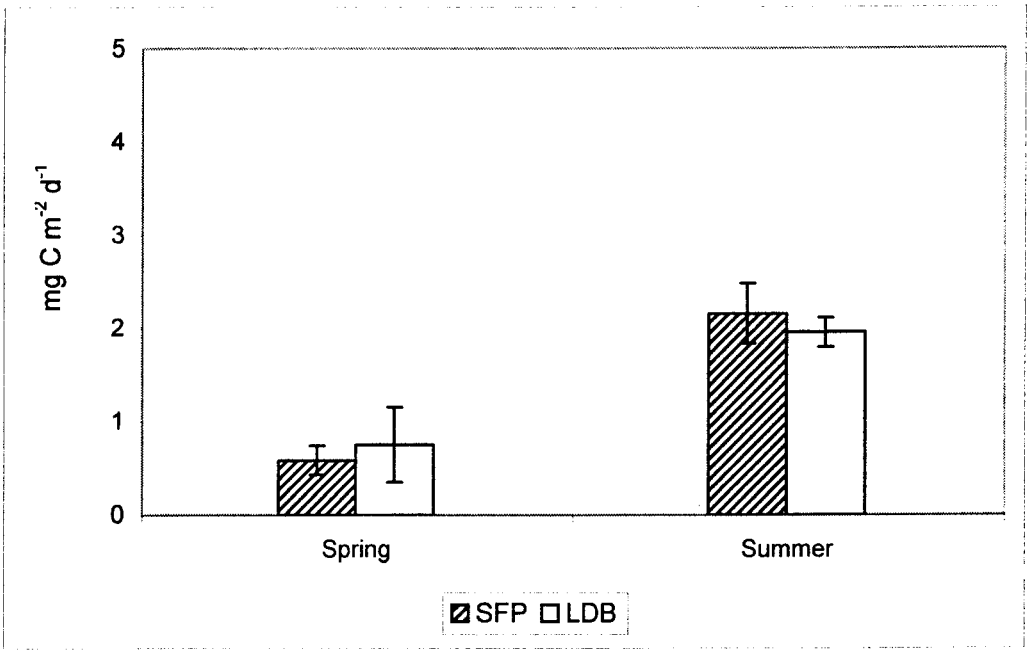


Figure 19: Seasonal mean (+/- 1 S.E.) daily primary production, g C m^{-2} d^{-1}, estimated from SFP and LDB techniques during 2001.

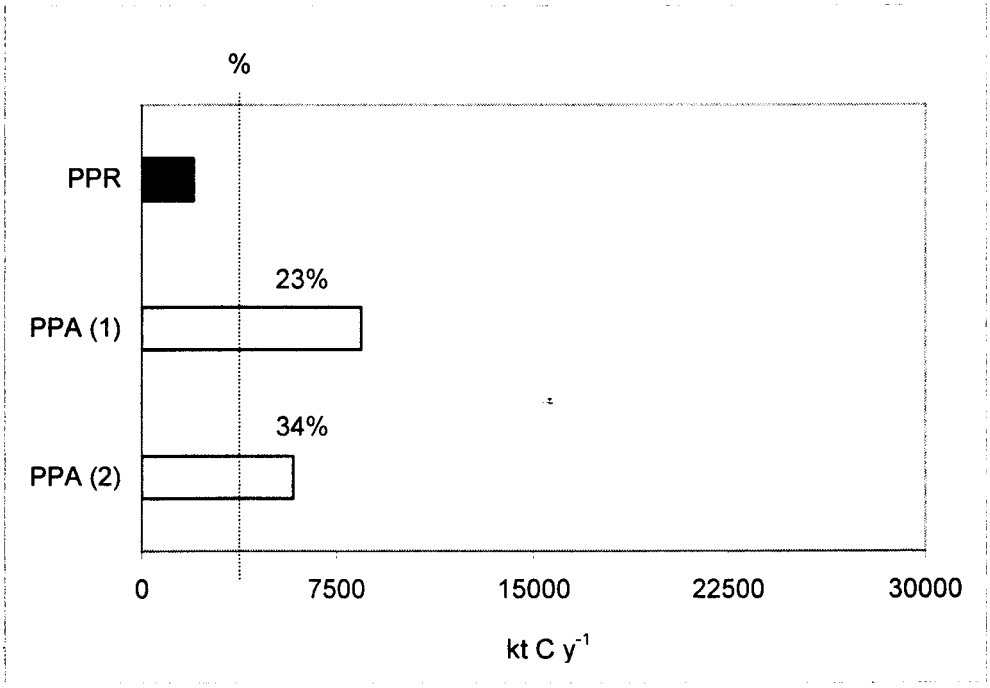


Figure 20: The lake-wide primary production required (PPR) to support a commercial catch of top predators compared to two estimates of primary production available. Units are kt C y^{-1}. PPA (1) is biased high assuming that west basin data are applicable to all of Lake Erie. PPA (2) accounts for observed differences in primary production in the central and eastern basins. Percentages (%) indicate the proportion of PPA consumed by PPR.

Discussion

Simple empirical models have been used as management tools in the Great Lakes with phosphorus loads identified as the single major stressor limiting primary production and algal standing crop (Vollenweider et al. 1974). Evidence presented in the Introduction suggested that multiple stressors were affecting the primary production regime of western Lake Erie. This discussion will examine the relative importance of known stressors that regulate primary production and will further explore the impact of reduced phosphorus loadings on both primary production and algal standing crop. The collective impacts of these findings will then be considered with respect to carbon dynamics and sustainable fisheries.

As there has been no discernable change in temperature in the Western Basin of Lake Erie since Burns' data from the 1970s (Burns, 1976), it is unlikely that the changes in phytoplankton composition and production potential are related to thermal stress. There has been, however, a marked change in the underwater light climate that was attributed to the zebra mussel (Holland, 1993). The vertical attenuation coefficient (ϵ_{par}) has decreased from 0.5 – 2 m^{-1} in 1978 (Wallen and Botek, 1984) to 0.3 – 1.1 m^{-1} in 2002 (this study). Considering that the change in ϵ_{par} is directly related to the decline in phytoplankton abundance reported by Nicholls and Hopkins (1993), it is possible that photosynthesis in Lake Erie, previous to the zebra mussel, was light limited as indicated in the earlier Vollenweider models where primary production was at or near saturation. Overall, based on the light penetration data available there has been approximately a two-

fold increase in the depth at which photosynthesis occurs in the western basin of Lake Erie.

The relative importance of phosphorus controls on primary productivity remains a question. The rationale behind the nutrient control program was quite simple. In the late 1960s and early 1970s, nitrogen was established as the nutrient limiting primary production in western Lake Erie (Vallentyne, 1974), a characteristic of eutrophic lakes. By reducing phosphorus loads, it was anticipated that phosphorus would become the limiting nutrient, which is characteristic of oligotrophic lakes. Therefore, if the nutrient control program was successful in reversing the trend of eutrophication, the west basin should be showing signs of phosphorus limitation.

There was no evidence of either phosphorus or nitrogen limitation based on our measurements of total phosphorus (Fig. 9) and nitrate (Fig. 11). The nutrient data suggest that although the basin has at least become less eutrophic than in 1970, it has not become oligotrophic as predicted when the phosphorus control program was implemented. Our observations of chlorophyll a and the phytoplankton community have revealed an algal community with a composition and relative abundance indicative of mesotrophic conditions.

Although target phosphorous loadings were met by the late 1970s (Lesht et al. 1991), target total phosphorus concentrations of 0.015 mg l^{-1} were rarely observed during this study and an historical analysis of summer mean concentrations, incorporating the data of Charlton et al. (1999), have indicated that this target has rarely been met (Fig. 21).

Phosphorus loadings in 2000 were estimated to be 4 519 t y^{-1} (Dolan, University of Wisconsin, *pers. comm.*), slightly below the target load of 5 000 t y^{-1}. Residual inputs from Lake Huron, however, push this figure up to 5 600 t y^{-1} (ibid). Even with phosphorus loading targets of the GLWQA being met, western Lake Erie has not become the oligotrophic phosphorus limited system that was predicted.

It has been shown that, in general, the phosphorus supply for lake plankton comes mainly from phosphorus regeneration and not external loadings (Hudson et al. 1999). This would suggest that a phosphorus-limited oligotrophic system in western Lake Erie will not be achieved for a long time via nutrient controls. Therefore, it is necessary to re-evaluate the endpoints of the nutrient control program with respect to limnological processes in order to determine what can be achieved in Lake Erie.

Total phosphorus (TP) concentrations, however, are likely not the most appropriate measure of phosphorus in the system since only a small fraction of it is biologically available as phosphate. Furthermore TP measurements are sensitive to sediment resuspension events, which drive up concentrations but not necessarily the biologically available fraction. Western Lake Erie is relatively shallow, with strong prevailing winds, soft bottom substrates and a well-mixed water column; hence it is very sensitive to sediment disturbance events as observed by Morrison et al. (2000). Resuspension likely explains the dramatic difference in TP concentrations observed in the fall of 2001 and throughout 2002. A better understanding of the factors regulating biologically available phosphorus and determining recycling rates of phosphorus within the phytoplankton community is needed.

Seasonal mean chlorophyll a concentrations in western Lake Erie showed significant variability between 1970 and 2002 (Fig. 22). Spring mean concentrations declined significantly ($P < 0.05$) between 1970 and 1993, 1998, and 2002, but not 2000 and 2001. Spring 2002 chlorophyll a was exceptionally low, <1 mg m^{-3}, but samples were only collected on one date (June 28) and were not representative of temporal trends. Summer chlorophyll a levels in all years were significantly lower ($P < 0.05$) than those observed in 1970. Fall concentrations showed significant differences ($P < 0.05$) between 1970 and both 1993 and 1998, however fall 2000 and 2001 concentrations were not significantly different ($P > 0.05$) from those reported in 1970. Overall, these results were consistent with the predicted impacts of phosphorus controls, given that nutrient controls were expected to reduce phytoplankton biomass as measured by chlorophyll a concentrations (Vollenweider et al. 1974).

Multi-year comparisons of spring and summer mean phytoplankton biomass in western Lake Erie are shown in Figure 23. These comparisons include pre-nutrient control data from 1970 (Munawar and Munawar, 1976), post-nutrient control and pre-zebra mussel data from 1983-1988 (Makarewicz et al. 1999), post zebra mussel data from 1989-1993 (ibid) and data from 2000 and 2001 (this study). The data have revealed that the largest decline in phytoplankton biomass coincided with the establishment of nutrient controls; the decline associated with the zebra mussel, deemed statistically significant by Makarewicz et al (1999), was relatively minor in comparison. There was some evidence that a considerable recovery has occurred since the mid 1990s. These observations indicate that zebra mussels were likely not controlling phytoplankton biomass. But it

must be remembered that Makarewicz et al.'s (1999) pre zebra mussel period includes the year 1988 in which mussels became established (Leach, 1993) and thus does not truly represent pre zebra mussel conditions. This makes it extremely difficult to separate the effects of the zebra mussels on the phytoplankton community from the long-term effects of nutrient controls (Munawar et al. 1999). Nevertheless, these findings are in contrast with Nicholls and Hopkins (1993), who found that zebra mussels played a much greater role in regulating phytoplankton densities than did phosphorus controls. Densities, however, are not biomass and the data sets are not directly comparable. Despite the importance of phytoplankton biomass to the overall health and functioning of Lake Erie, there has been little effort to quantify changes in composition and abundance of phytoplankton species.

In assessing the statistical significance of changes in phytoplankton biomass, one has to be mindful that biomass is estimated from microscopic counting of algal cells. Even though precision increases with the number of organisms counted, accuracy is only +/- 50% since cells that were living at the time of preservation are virtually indistinguishable from those which are moribund (Lund et al. 1958). This is particularly important when comparing the work of different researchers.

Using Lund et al.'s (1958) estimate of +/- 50% as the experimental error, spring mean phytoplankton biomass indicated a significant ($P < 0.05$) decline from 7.1 g m^{-3} in 1970 to 2.0 g m^{-3} in the 1983-88 period. There was no significant decline ($P > 0.05$), between the immediate pre (1983-88) and post (1989-93) zebra mussel periods. There was a significant ($P < 0.05$) increase in biomass from 1.3 g m^{-3} in 1990-94 to 4.9 g m^{-3} in 2000

and 4.6 g m^{-3} in 2001, which in turn were not significantly different ($P > 0.05$) from 1970. Summer mean phytoplankton biomass did not show any significant changes using this approach. Despite having assembled the most temporally complete portrait of the phytoplankton community in western Lake Erie, Nicholls and Hopkins (1993) computed their findings in Areal Standard Units (ASU) ml^{-1}, which were not compatible with any of the other data sets.

Several important points emerge from Figure 23. First, nutrient controls appear to have had a greater impact on phytoplankton biomass than zebra mussels. Second, the impact of reduced phosphorus was observed primarily in the spring indicating that either spring run off or nutrient recycling play a critical roll in nutrient loadings. Third, the phytoplankton community must have adapted to reduced phosphorus loadings or zebra mussel grazing, since it was shown that phosphorus loadings have not increased in 2000. The structural composition of the phytoplankton community needs to be examined in closer detail. Fresh weight biomass and chlorophyll a are not sufficient measures to quantify how the phytoplankton community responds to phosphorus controls or increased grazing by zebra mussels.

Evidence that grazing and selective feeding by zebra mussels has altered the structure of phytoplankton communities throughout the Great Lakes has been shown in several studies (e.g. Holland, 1993; Nicholls and Hopkins, 1993; Fahnenstiel et al. 1995; Munawar and Munawar, 1999; Vanderploeg et al. 2001). In western Lake Erie, Munawar and Munawar (1999) found that in addition to a sharp decline in biomass between July 1970 and July 1992, Chlorophyta had replaced Diatomeae as the dominant taxon. When

combined with July data from the current study (Fig. 24), it was evident that there was considerable inter-annual variation in both composition and biomass, even over the course of a single year. Spring and summer composition for 1970, 2000 and 2001, by taxa, were virtually indistinguishable from each other (Fig. 25). A finer taxonomic resolution is needed to address whether or not a change in the structure of the phytoplankton community has occurred.

At the *genus* level, there was evidence that a structural change had occurred. Tables 2 and 3 list common genera, those representing at least 5 % of the biomass, from 2000 and 2001 respectively. The diatoms *Fragillaria*, *Stephanodiscus*, *Melosira* and the chlorophyte *Pediastrum* were common in 1970 (Munawar and Munawar, 1976), 2000 and 2001. Other common genera from 1970 (ibid), including *Gymnodinium*, *Coscinodiscus*, *Aphanizomenon*, *Ceratium*, *Staurastrum* and *Rhodomonas* had declined to less than 5 % of the biomass. Of special note is *Rhodomonas*, which was reported as common in the spring and summer of 1970, but not in 2000 or 2001. *Rhodomonas*, however, did dominate counts in both 2000 and 2001 but due to its small size did not contribute a large portion of the biomass.

In 2000 and 2001, the chlorophyte *Chlamydomonas* was common in virtually all samples. Similarly, the diatom *Cyclotella*, the cyanophytes *Holopedium* and *Microcystis* and the dinophyte *Peridinium* were common in these years but not in 1970. The emergence of *Microcystis* in the Great Lakes has been attributed to selective feeding by the zebra mussel (Vanderploeg et al. 2001), which has reportedly made conditions beneficial for these toxic algae. In western Lake Erie, this was not observed since *Microcystis* was

reported as a common species in the 1930's (Tiffany, 1934) more than 50 years before the arrival of the zebra mussel and 40 years before the establishment of nutrient controls. In fact, this point can be made about the other common genera in 2000 and 2001. These findings were consistent with both Munawar and Munawar (1999) and Makarewicz et al. (1999) who observed that the phytoplankton community reflects more mesotrophic conditions, but a still finer taxonomic resolution, i.e. to species, would be required to make a conclusive statement from the current data set.

In contrast to the situation with *Rhodomonas*, i.e. high abundance and low biomass, was the case of the chlorophyte *Volvox*, which was reported as common in three samples in 2001. In fact, only three were observed which offers no statistical precision but, due to their large size, their contribution to the biomass cannot be ignored. Biomass alone offers a statistically biased portrait of the phytoplankton community; the same point can be made about abundance data, or counts, for similar reasons. This is why any true portrait of the phytoplankton community must include other independently measured parameters, like primary productivity, and why size fractionation serves a useful analytical tool for lake and fishery management models.

By re-examining previously reported phytoplankton biomass data from 1970 (Munawar and Munawar, 1976), 1983-1993 (Makarewicz et al. 1999) along with current data from this study, it was shown that, all other things being equal, nutrient controls likely had a greater impact on biomass in the western basin than the filtering impacts of zebra mussels. This current study indicates, however, that biomass has recovered since the mid

1990s to levels similar to 1970. These recent observations indicate that the algal standing crop has undergone a structural adaptation since the imposition of nutrient controls.

This structural adaptation, however, should not be considered as inconsistent with the findings of Nicholls and Hopkins (1993), who observed that grazing by zebra mussels was more important to regulating phytoplankton densities than were nutrient controls. Nicholls and Hopkins (1993) had anticipated that smaller, more productive algae would come to dominate primary production. There was evidence of this our measurements of size fractionated primary productivity in 2000 and 2001, where algae in the 2 – 20 μm fraction dominated productivity measurements in all samples (Fig. 15). The individual factors that make up phytoplankton dynamics, e.g. chlorophyll a, biomass, density, abundance, productivity and production, cannot be viewed in isolation from each other; it is imperative that their collective synergies be understood. It is also imperative that the impact of multiple stressors on phytoplankton dynamics be considered.

Both Munawar and Munawar (1999) and Makarewicz et al. (1999) reported the presence of more oligotrophic genera in the 1990s, a trend that was confirmed in our study. The phytoplankton community is showing signs of adaptation to mesotrophic and oligotrophic conditions, a trend also evidenced by the decline in chlorophyll a concentrations, but primary production has not responded as predicted by the empirical models of Vollenweider et al. (1974).

Both SFP and LDB techniques for measuring primary productivity were run simultaneously during the spring and summer of 2001, albeit at different sites and with

different sampling methods. SFP was deployed on depth-integrated samples from sites W5, W6, W7 and W8 and LDB was deployed on discrete-depth samples at MSI. In spite of these, no significant differences ($P > 0.05$) in mean primary productivity were observed between techniques (Fig. 17). Average daily rates of primary production also showed no significant differences ($P > 0.05$) between techniques (Fig. 18). These observations indicate that *in situ* (LDB) incubations are comparable to constant light incubations (SFP). The similarity between the two techniques supported the use of historic data sets to examine long term trends in primary production in the western basin of Lake Erie.

Annual primary production for 2001 was 351 g C m^{-2} when calculated from SFP data and 350 g C m^{-2} when calculated from LDB data. This provides further evidence that spatial and temporal variability among sampling regimes deployed in this study were insignificant when estimating overall productivity of the western basin.

Primary productivity measurements from May 4, 2000 and May 29, 2001 supported the observations of Munawar et al. (1999), that spring primary productivity has declined tenfold, from approximately 85 mg C m^{-3} hr^{-1} in 1988 to < 8 mg C m^{-3} hr^{-1} (Fig. 26). This decline in spring primary productivity coincided with the arrival of the zebra mussel although other factors must be considered. The 1988 measurement was taken in April and the 1993 - 2001 measurements were taken between May and June. It is possible that later sampling dates circumvented the observation of a spring bloom.

It is worth noting that the range of primary productivity values in the spring 1988 – 2001 observations were consistent with the range of values observed between 2000 and 2001. It is possible that a spring algal bloom was missed during the sampling of spring 1993 - 2001. More frequent temporal coverage, recommended on a weekly basis, is required to offer a true assessment of the changes in primary productivity and carbon dynamics in Lake Erie.

Average spring primary productivity in the April – June period for 1978 was reported at 39.8 mg C m^{-3} hr^{-1} (Wallen and Botek, 1984). Their technique was similar to the LDB technique deployed in this study except that a variable light incubator was used in place of *in situ* incubations. The 1978 values were four fold higher than the spring mean productivity of 10 mg C m^{-3} hr^{-1} in 2001 and 8.7 mg C m^{-3} hr^{-1} in 2002 (Fig. 27). This change was significant ($P < 0.05$) and it is concluded that spring primary productivity has declined by approximately 75% since 1978.

This decline in spring primary productivity has implications for water quality management. First, phosphorus loadings in 1978 of 11 928 t (Lesht et al., 1991) and phytoplankton densities of 4508 ASU ml^{-1} (Nicholls and Hopkins, 1993) were similar to those in the early 1970s when nutrient controls were put in place. Second, April 1988 was shortly before zebra mussels were first reported in the western basin (Leach, 1993). The peak rate of primary productivity in spring 1978 was 71.0 mg C m^{-3} hr^{-1} (Wallen and Botek, 1984) and was quite similar to the 87.3 mg C m^{-3} hr^{-1} observed in spring 1988 by Munawar and Munawar (1999). This historical pattern of spring primary productivity implies that phosphorus controls had no measurable impact on primary productivity prior

to the arrival of the zebra mussel. Unfortunately, the data set required to test this particular hypothesis does not exist.

Despite the changes observed in spring primary productivity between 1978 and 2002, summer mean primary productivity revealed no temporal trend (Fig. 27) ranging from 22.5 mg C m^{-3} hr^{-1} in 2002 to 30.7 mg C m^{-3} hr^{-1} in 1978. No historic data were available for fall comparisons. Nevertheless, the available data have demonstrated that significant changes in primary productivity have occurred in the spring.

Average spring primary production (g C m^{-2} d^{-1}) did not show the same trend as spring primary productivity. Glooschenko et al. (1974a) measured spring production at 1.0 g C m^{-2} d^{-1} compared to 0.9 g C m^{-2} d^{-1} in 1993 (Dahl et al. 1995) and 0.3 to 0.9 g C m^{-2} d^{-1} in 2000, 2001 and 2002 (Fig. 28a). The lowest value, spring 2000, was based on a single sample in early May when production is typically low. This is only an empirical comparison, but it does suggest that spring daily primary production rates (areal) in the west basin have remained constant while hourly rates (volumetric) have declined significantly.

The difference in temporal trends for primary productivity and production is consistent with the observation that euphotic depth (Z_{eu}) has increased and that photosynthesis is occurring deeper in the water column. Consequently, areal rates of primary production have remained stable while volumetric rates of primary productivity have declined.

Average summer primary production ranged from 0.9 – 2.2 mg C m^{-2} d^{-1} for 1970, 1993, 2000, 2001 and 2002 (Fig. 28b), and there are no significant differences in summer primary production from 1970 to 2002 ($P > 0.05$). This similarity in summer production over time suggests that summer primary productivity was limited by different factors than spring productivity. Mean fall primary production rates ranged from 0.3 – 1.5 mg C m^{-2} d^{-1} for 1970, 1993, 2000 and 2001 (Fig. 28c), but there were too few observations to make a statistically meaningful comparison. In the final analysis, there was no evidence to conclude that there have been any significant changes in daily primary production rates between 1970 and 2002.

Vollenweider et al. (1974) developed simple empirical models for managing phosphorus loads and regulating primary production. These were intended to help alleviate eutrophic conditions occurring in the Great Lakes, particularly western Lake Erie. Much of the evidence presented in this study indicates that phosphorus loadings alone have not been regulating primary production in the west basin. The question of whether or not these simple empirical models are still valid management tools needs to be addressed.

Phosphorus loadings into the western basin for 2000, the only year of this study period for which data were available, were 1.4 g TP m^{-2} y^{-1} (Dolan, *pers com*). This was substantially lower than the 6.0 g TP m^{-2} y^{-1} reported in 1970 (Vollenweider et al. 1974) and indicates that the GLWQA has been successful in reducing loads. Based on the model of Vollenweider et al. (1974):

$$\Sigma a=420[10(TP)^{0.6}\ (9+10(TP)^{0.6})^{-1}], \text{ where}$$

Σa = annual primary production, and

TP = total phosphorus loadings.

The projected annual primary production for 2000 is 242 g C m^{-2} y^{-1} and for 1970 is 321.3 g C m^{-2} y^{-1}. This compares to observed values of 372 g C m^{-2} y^{-1} in 2000 and 340 g C m^{-2} y^{-1} in 1970 (Fig. 29a), supporting the conclusion that primary production is not simply related to phosphorus loadings. These observations raise questions as to the use of empirical models as management tools in systems where multiple stressors are known to operate. Future research must be directed at establishing the processes and mechanisms that regulate primary production in the Great Lakes.

The use of empirical models is further questioned when we consider the second model of Vollenweider et al. (1974):

$\Sigma a=420\ [1.15(Chl)^{1.33}(9+1.15(Chl)^{1.33})^{-1}]$, where

Σa = annual primary production, and

Chl = annual mean chlorophyll a concentration.

Despite the agreement shown in 1970, there is no agreement in 1993, 2000, 2001 and 2002 measurements (Fig. 29b). Predicted levels of annual primary production from 1993 - 2002 based on observed levels of chlorophyll a (Table 4) ranged from 171 to 260 mg C m^{-2} y^{-1}, compared to observed measurements of 281 to 372 mg C m^{-2} y^{-1} in the same period. Primary production has remained at eutrophic levels while algal standing crop, measured as chlorophyll a, has declined to mesotrophic levels.

The predicted level of primary production in 2000 from the first model, based on phosphorus loadings of 1.4 g TP m^{-2} y^{-1}, was 242.0 g C m^{-2} yr^{-1} and the corresponding annual average chlorophyll a concentration from the second model would be 5.9 mg m^{-3}, which was very close to the observed value of 5.6 mg m^{-3} (+/- 0.25). This observation provides further evidence that nutrient controls have reduced the standing crop of phytoplankton, measured as chlorophyll a, as intended. But it also suggests that these simple empirical models are no longer sufficient as management tools to predict primary production and biomass in multiple stressed systems.

A change in the photosynthetic efficiency (mg C fixed per unit chlorophyll a per unit time) of the standing crop has occurred which questions the use of Vollenweider's empirical model that does not compensate for adaptations by the phytoplankton. Mean summer (June to September) carbon assimilation rates have increased from 13 mg C mg Chl^{-1} d^{-1} in 1970 to 21 – 55 mg C mg Chl^{-1} d^{-1} between 1993 and 2002 (Fig. 30a). The change is significant for all years except 2000 ($P < 0.05$), but the 2000 data set contains only 3 samples taken between late August and mid September. These comparisons were made using 1970 primary production data from Glooschenko et al. (1974a) and chlorophyll a data from Glooschenko et al. (1974b); 1993 data were from Dahl et al. (1995). This same data set, used here to estimate photosynthetic efficiency, can also be used to estimate carbon turnover times.

The carbon cycle is the most basic of ecosystem functions, inextricably linked to energy flows and therefore crucial to any understanding of food webs and contaminant dynamics. Mean summer (June to September) carbon turnover times have decreased, from 4.5 days

in summer 1970 to 2 days in summer 2002 (Fig. 30b). Faster carbon turnover times reflect the lower standing crop (measured as chlorophyll a as a measure of biomass) as evidenced by increased water clarity and a constant rate of areal primary production. This rapid replacement of the phytoplankton biomass supports Epplett et al.'s (2000) and Haffner and Kozlawski's (1999) postulation that high algal growth rates are regulating contaminant dynamics by the process of trophic dilution. The increase in carbon turnover rates, precipitated by reductions in chlorophyll a and elevated levels of primary production are helping to maintain ecosystem health.

The reliability of current estimates of primary production needs to be improved in order to provide more relevant management tools. Current models in use the Great Lakes, specifically Vollenweider (1969) and Fee (1977) are based on carbon uptake experiments that are relatively short (1-4 hours) in duration. Because of the short duration, ^{14}carbon uptake experiments do not account for changes in photosynthetic activity that may result from either variations in incoming solar radiation or differences in photosynthetic activity among phytoplankton species. As a result, the experimental error, assumed to be large (Vollenweider et al. 1974), is incalculable over the course of a season and even more so over the course of a year. A better understanding of the photosynthetic responses of phytoplankton to changes in irradiance is needed to improve these models, which would in turn provide managers with a better understanding of the energy requirements of the pelagic food web.

Achieving a sustainable fish catch is a critical goal for fisheries managers. This goal implies managing the catch within the context of a sustainable, productive food web, i.e.

taking an "ecosystem approach", and primary production is the genesis of all food webs. The total lake wide commercial fish catch from Lake Erie in 1998 was 17.8 million kg (MacGregor, 1999). If this catch were dominated by top predators (e.g. walleye: *Stizostedion vitreum*) with a trophic level of at least 4, than the primary production required to sustain it would be 1 976.9 kt C y^{-1} based on the model of Pauley and Christensen (1995). Any potential reliability problems with catch data (Alverson et al. 1994; Garcia and Newton, 1997) were ignored in this analysis. This model yields a rather conservative estimate of PPR since neither by-catch nor the sport fisheries were considered.

The best-case estimate of available primary production (PPA) for Lake Erie is 8, 460.2 kt C y^{-1}, when west basin annual primary production rates are applied lake-wide. PPR, in this circumstance, is 23.3% of the available primary production, an amount virtually identical to the global average of 23.6% for freshwater systems (Pauley and Christensen, 1995) and more ominously, consistent with the PPR of the world's most exploited and endangered fisheries. More foreboding, this is an overly optimistic estimate of PPA because it assumes that primary production levels in the central and eastern basins were equivalent to the west. This assumption likely overestimates PPA since previous studies (Glooschenko et al. 1974; Dahl et al. 1995) have shown that west basin levels of primary production have been significantly higher than the others.

A more realistic estimate of lake wide PPA is 5, 834.3 kt C y^{-1}, which results in a PPR that is 33.9% of the available primary production. This was calculated using 1970 annual

primary production data (Vollenweider et al. 1974) under the assumption that primary production in all three basins has not changed significantly since then.

A sustainable fishery of top predators in Lake Erie would likely require a major reduction in PPR relative to PPA. The exact magnitude of the reduction in PPR needed is not known, but average PPR for global fisheries was 8 % of PPA (Strathman, 1967; DeVooys, 1979; FAO, 1993; Jarre-Teichmann and Christensen, 1995); Vitousek et al. (1986) put this figure at 2%. Nevertheless, reducing PPR in Lake Erie while maintaining a catch of top predators will necessarily involve increasing primary production. Otherwise, the average trophic level of the catch would have to be decreased (Pauley et al. 1998).

Assuming that a reduction of PPR to 8% of PPA is the minimum required for a sustainable fishery in Lake Erie, than primary production would have to be increased to 24 711.3 kt C y^{-1} in order to sustain the catch with a PPR of 1, 976.9 kt C y^{-1} (Fig. 31). Primary production in each of the three basins would have to exceed 975 g C m^{-2} y^{-1}, an amount that is more than double the theoretical global maximum established by the empirical models of Vollenweider et al (1974). Griffiths (1999) argued that a commercial catch of top predators could be maintained by relaxing the nutrient control provisions of the GLWQA and thereby increasing primary production. Manipulating primary production, however, is not a realistic management objective, since primary production is already occurring at saturation levels in western Lake Erie. In fact this study demonstrates that phosphorus does not control primary production and that it has remained unchanged despite a 30 year, bi-national effort to control eutrophication.

A commercial catch of top predators is not sustainable under Pauley and Christensen's (1995) model, a fact that has been borne out time and again by the collapse of top predators in Lake Erie (Nepszy, 1999). In order to have a sustainable catch of 17.8 million kg, the average trophic level of the catch would have to be 3.4 (Fig. 32). This trophic level would be consistent with a fishery composed of yellow perch, whitefish, rainbow smelt and white bass among others. All of these species are an important part of the Lake Erie commercial fishery (MacGregor, 1999; Nepszy, 1999). The implication is that we are already "fishing down the food web" (Pauley et al. 1998) which does not bode well for a healthy sustainable fishery in Lake Erie.

Fisheries management, like water quality management, needs to be considered within the context of multiple stressors. Current management practices do not incorporate the primary production required to sustain a catch. The challenge for fisheries managers is to understand the primary production requirements of the fishery and use this knowledge to develop a sustainable catch regime.

Table 4: Observed levels of chlorophyll a (mg m^{-3}) and observed annual primary production (g C m^{-2} y^{-1}) compared to predicted levels of primary production based on Vollenweider, Munawar and Stadelmann (1974).

Year	**Average Chlorophyll a** (mg m^{-3})	**Observed Primary Production** (g C m^{-2} y^{-1})	**Predicted Primary Production** (g C m^{-2} y^{-1})
1970	11.0	340	318
1993	3.6	281	171
2000	5.6	372	234
2001	6.8	351	260
2002	4.2	325	194

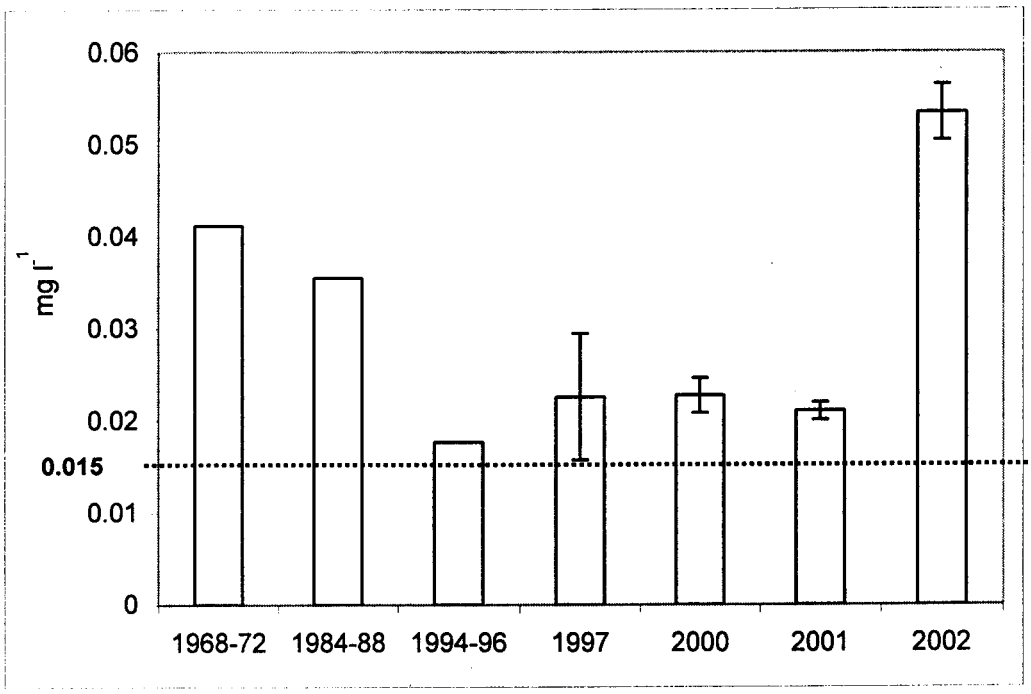
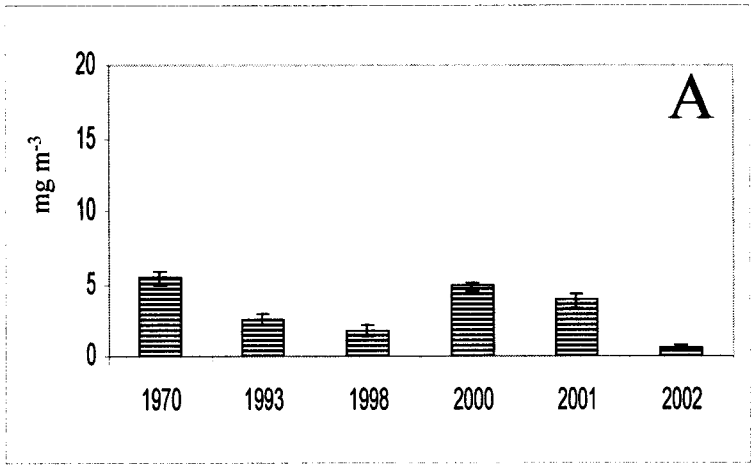
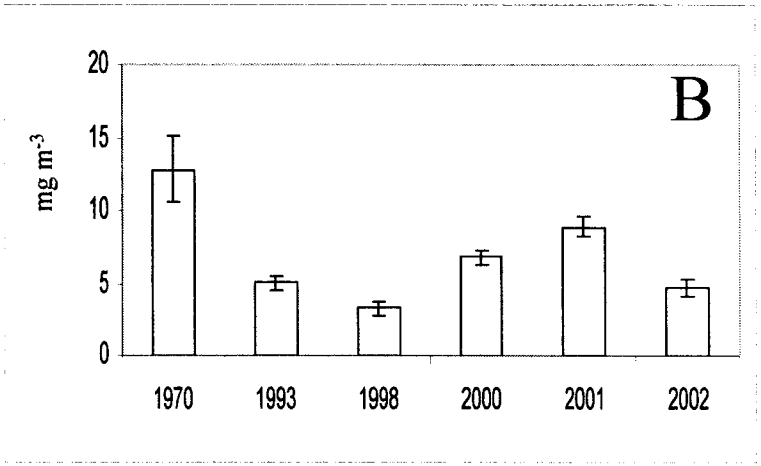


Figure 21: June to September mean (+/- 1 S.E.) total phosphorus concentrations, mg l^{-1}. 1968-1997 data are from Charlton et al. (1999), 2000-2002 data are from this study. GLWQA target concentration is indicated in boldface.





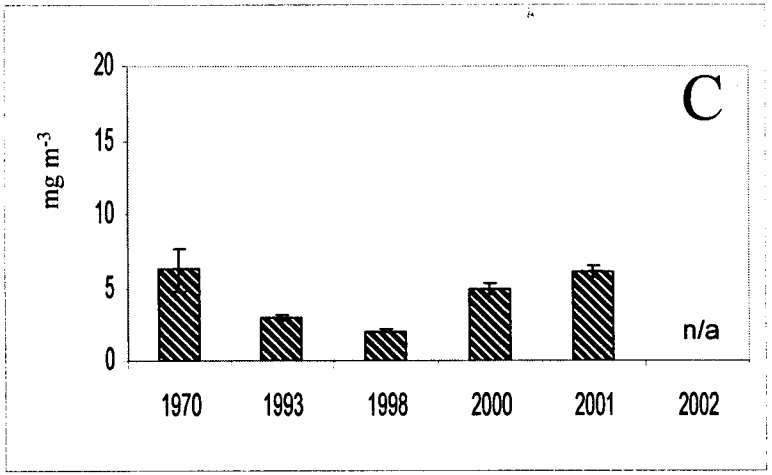


Figure 22: Mean (+/- 1 S.E.) chlorophyll a concentrations, mg m^{-3} for A: spring, B: summer and C: fall. 1970 data are from Glooschenko et al. (1974b), 1993 data are from Dahl et al. (1995), 1998 data are from McDougall et al. (2001), 2000-2002 data are from this study.

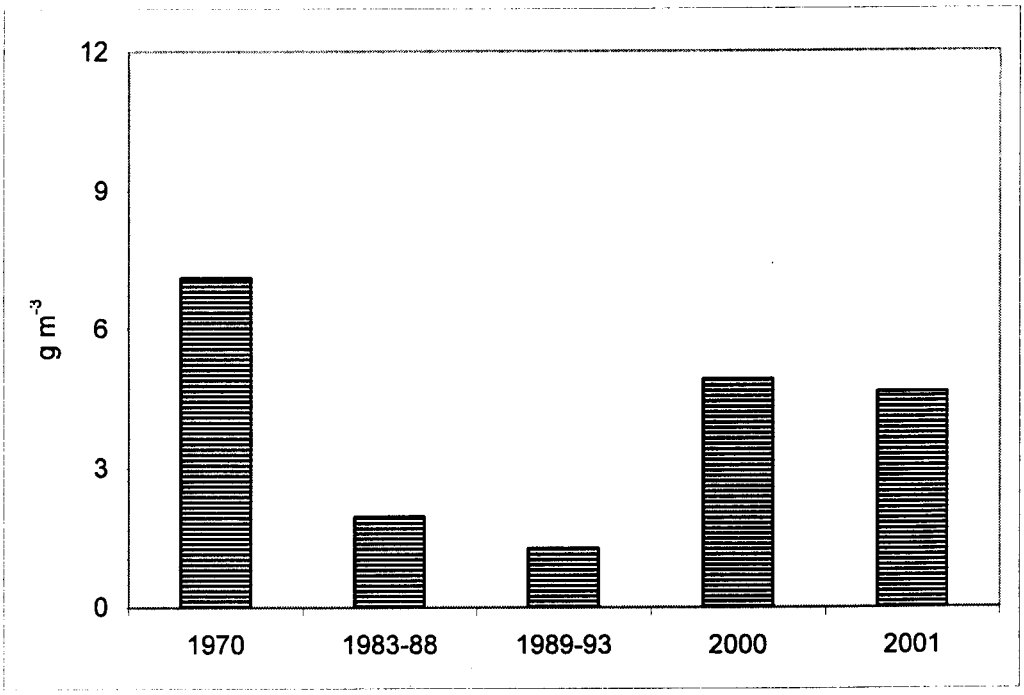


Figure 23a: Spring mean phytoplankton biomass, g m^{-3}. 1970 data are from Munawar and Munawar (1976), 1983 – 1993 data are from Makarewicz et al. (1999), 2000 and 2001 data are from this study.

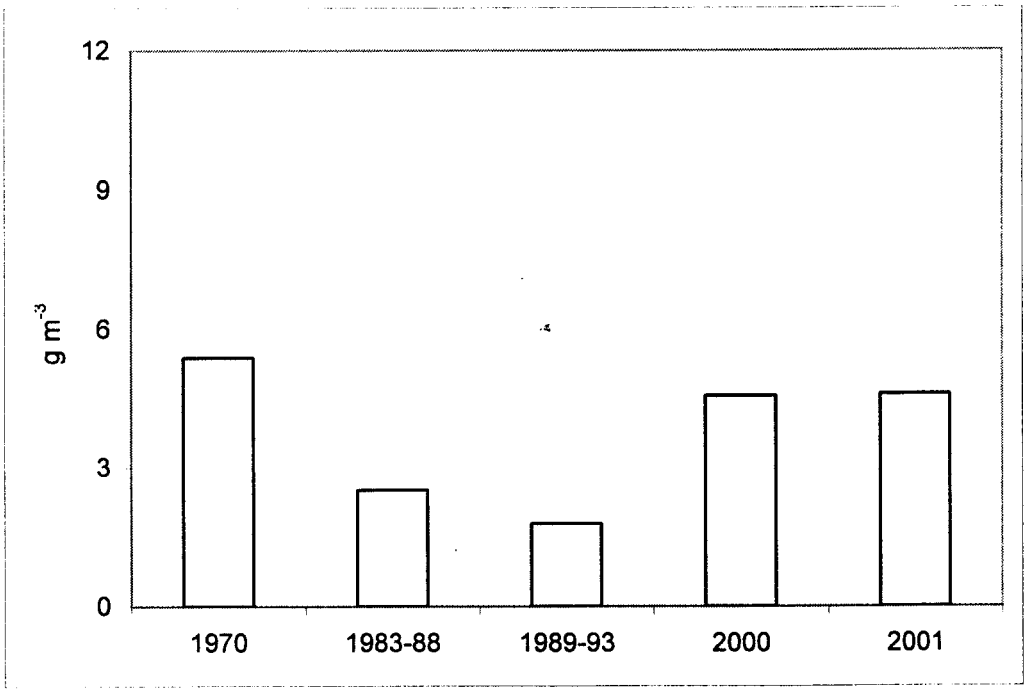


Figure 23b: Summer mean phytoplankton biomass, g m^{-3}. 1970 data are from Munawar and Munawar (1976), 1983 – 1993 data are from Makarewicz et al. (1999), 2000 and 2001 data are from this study.

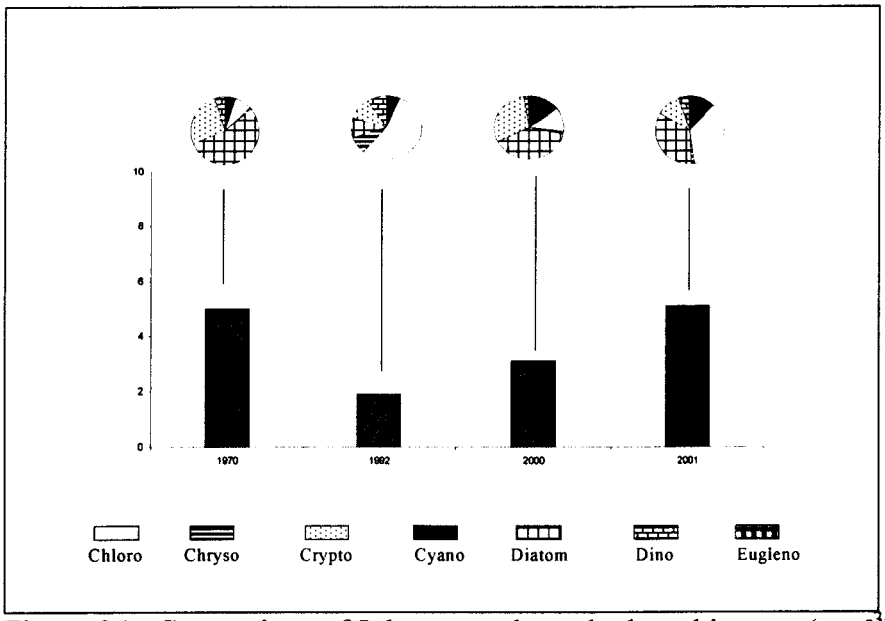


Figure 24: Comparison of July mean phytoplankton biomass (g m^{-3}) and % taxonomic composition (by weight). 1970 data are from Munawar and Munawar (1996), 2000-2001 data are from this study. Chlor = Chlorphyta, Chryso = Chrysophyceae, Crypto = Cryprophyceae, Cyano = Cyanophyta Diatom = Diatomeae, Dino = Dinophyceae and Eugleno = Euglenophyceae.

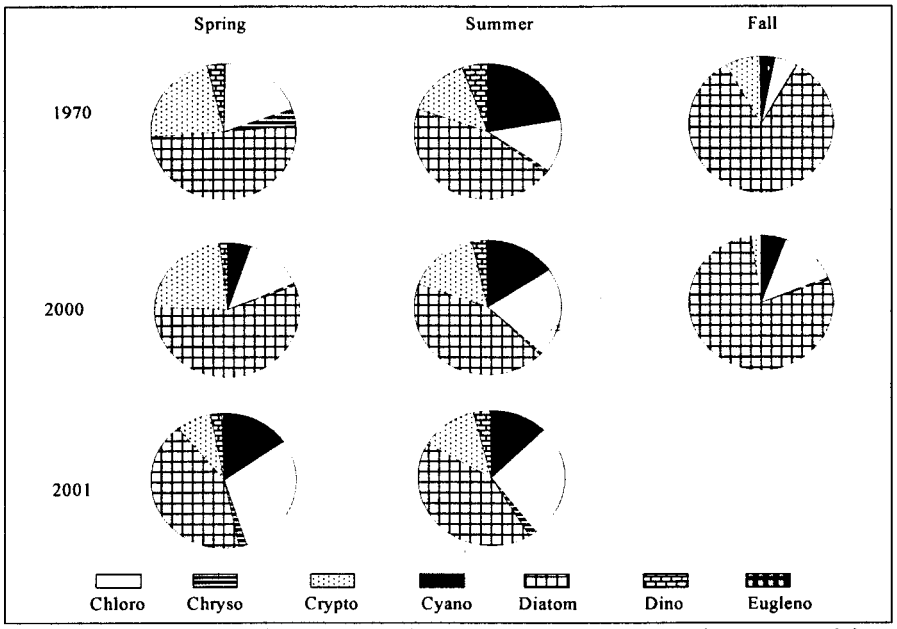


Figure 25: Seasonal mean % phytoplankton taxonomic composition (by weight) for 1970, 2000 and 2001. 1970 data are from Munawar and Munawar (1976), 2000-2001 data are from this study. Chlor = Chlorphyta, Chryso = Chrysophyceae, Crypto = Cryprophyceae, Cyano = Cyanophyta Diatom = Diatomeae, Dino = Dinophyceae and Eugleno = Euglenophyceae.

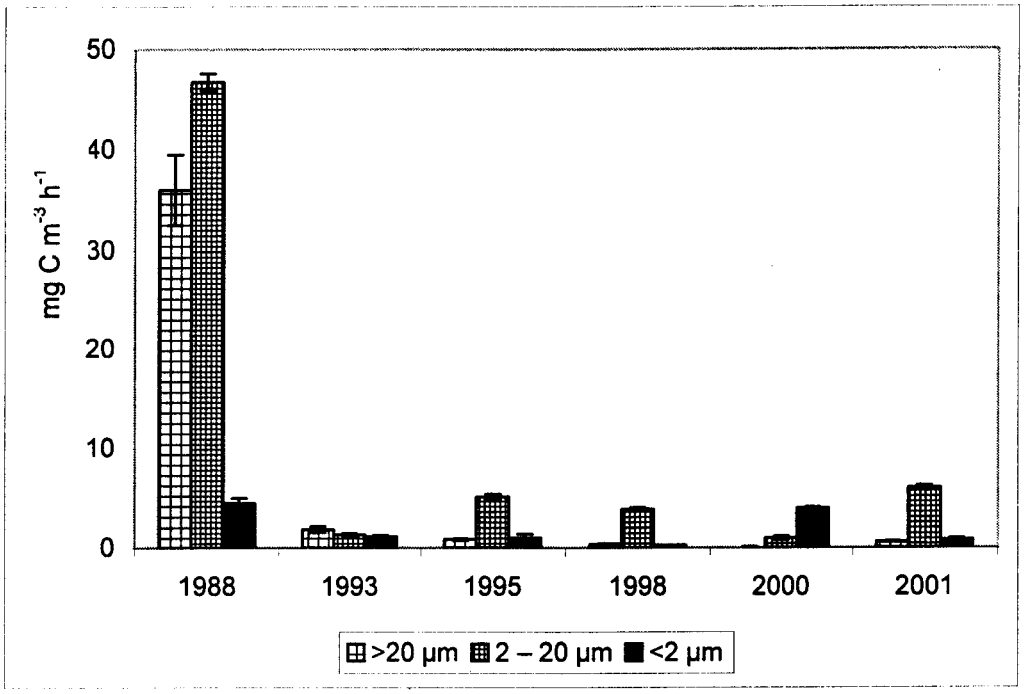


Figure 26: Spring mean (+/- 1 S.E.) primary productivity, mg C m^{-3} h^{-1} using SFP. 1988-1998 data are from Munawar et al. (1999), 2000 and 2001 data are from this study.

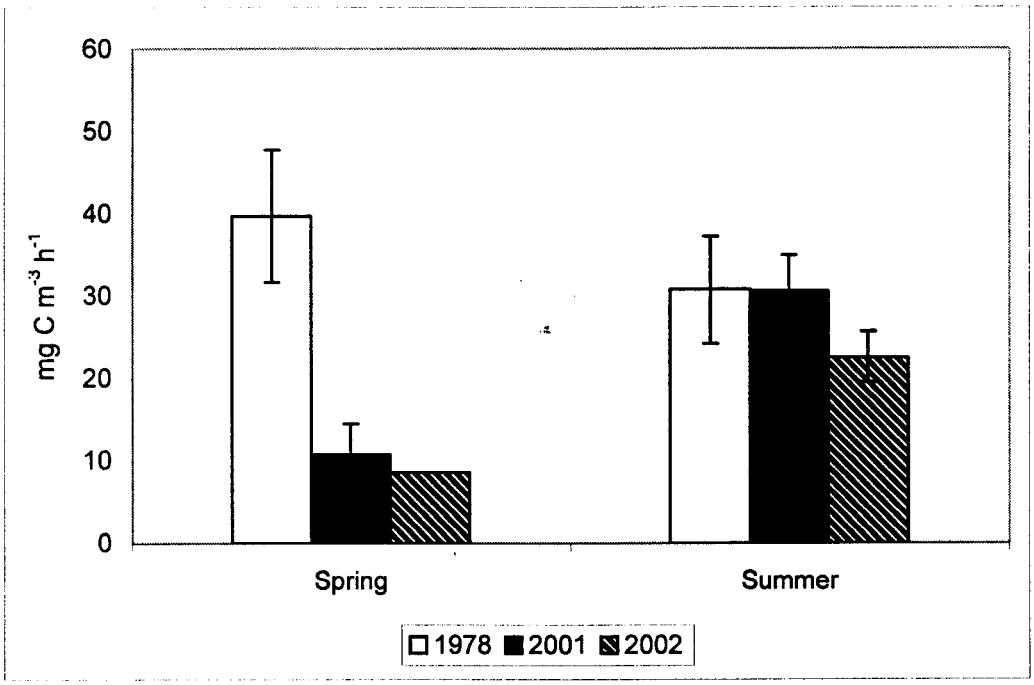


Figure 27: Seasonal mean (+/- 1 S.E.) primary productivity, mg C m^{-3} h^{-1}. 1978 data are from Wallen and Botek (1984), 2001-2002 data are from this study.

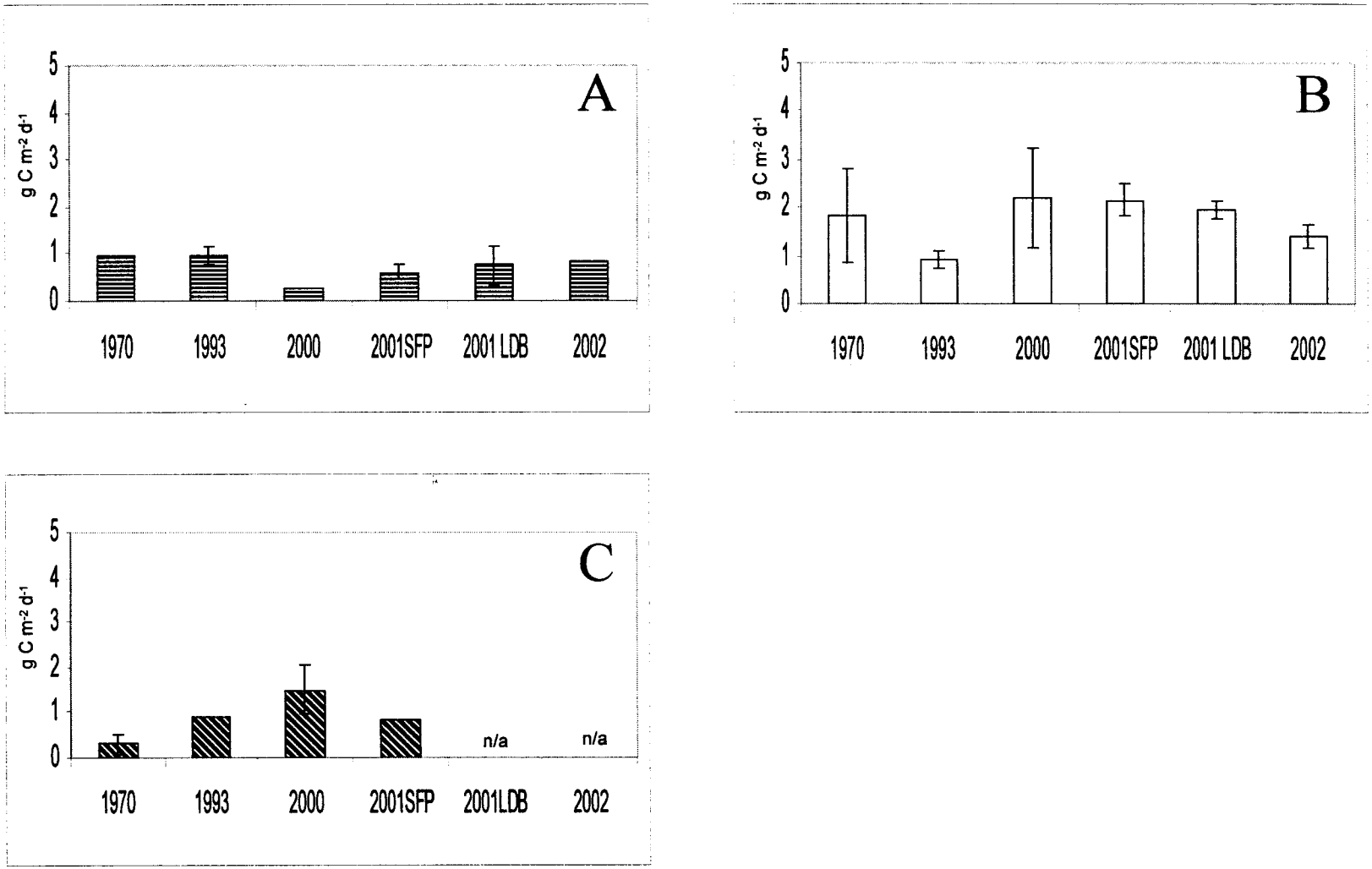


Figure 28: Daily mean (+/- 1 S.E.) primary production, g C m^{-2} d^{-1}, for A: spring, B: summer and C: fall. 1970 data are from Glooschenko et al. (1974), 1993 data are from Dahl et al. (1995) and 2000 - 2002 data are from this study

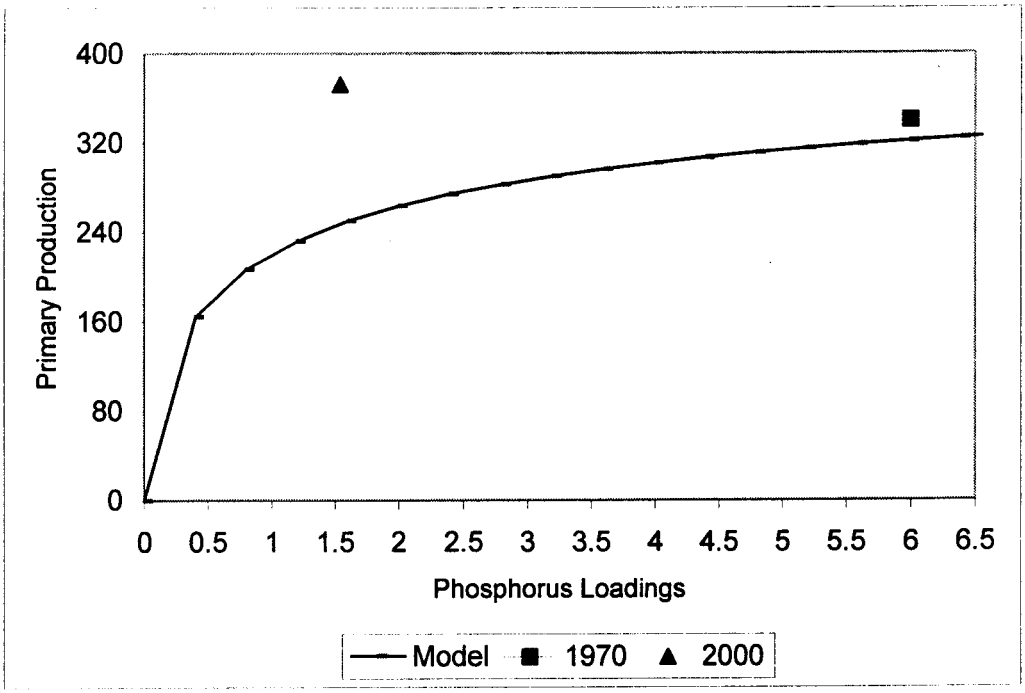


Figure 29a: Relationship between phosphorus loadings (g TP m^{-2} y^{-1}) and primary production (g C m^{-2} y^{-1}): $\Sigma a=420[10(TP)^{0.6}(9+10(TP)^{0.6})^{-1}]$ (Vollenweider, Munawar and Stadelmann, 1974). 2000 TP is from Dolan (*pers. com.*) 2000 PP is from this study.

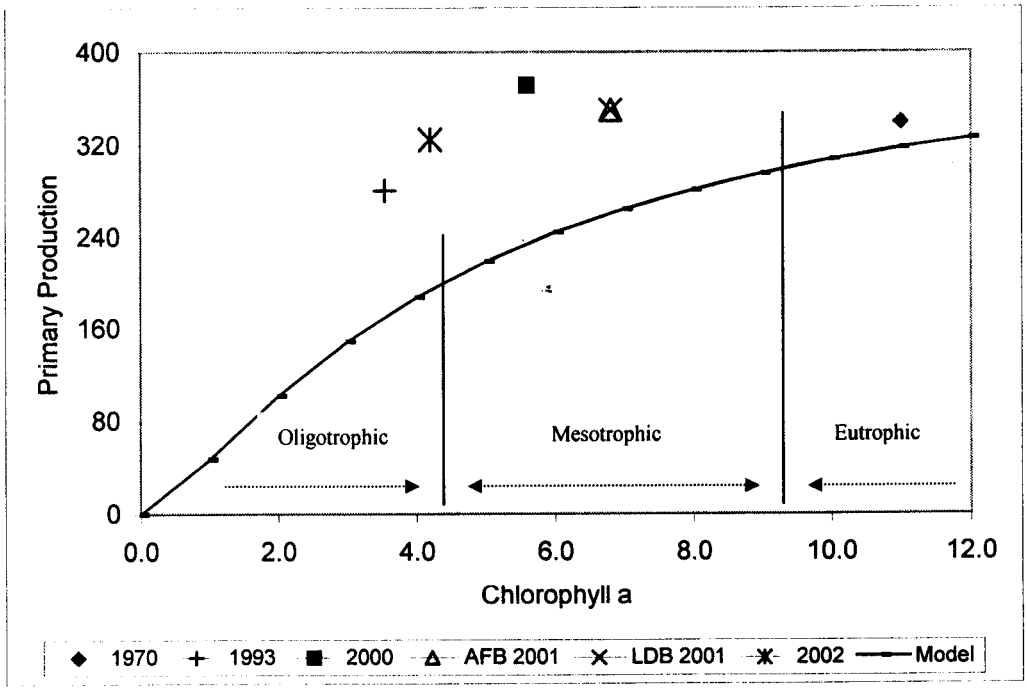


Figure 29b: Relationship between average chlorophyll a (mg m^{-3}) and primary production (g C m^{-2} y^{-1}): $\Sigma a=420\ [1.15(Chl)^{1.33}(9+1.15(Chl)^{1.33})^{-1}]$ (Vollenweider, Munawar and Stadelmann,1974). 1993 data are from Dahl et al. (1995) and 2000-2002 data are from this study.

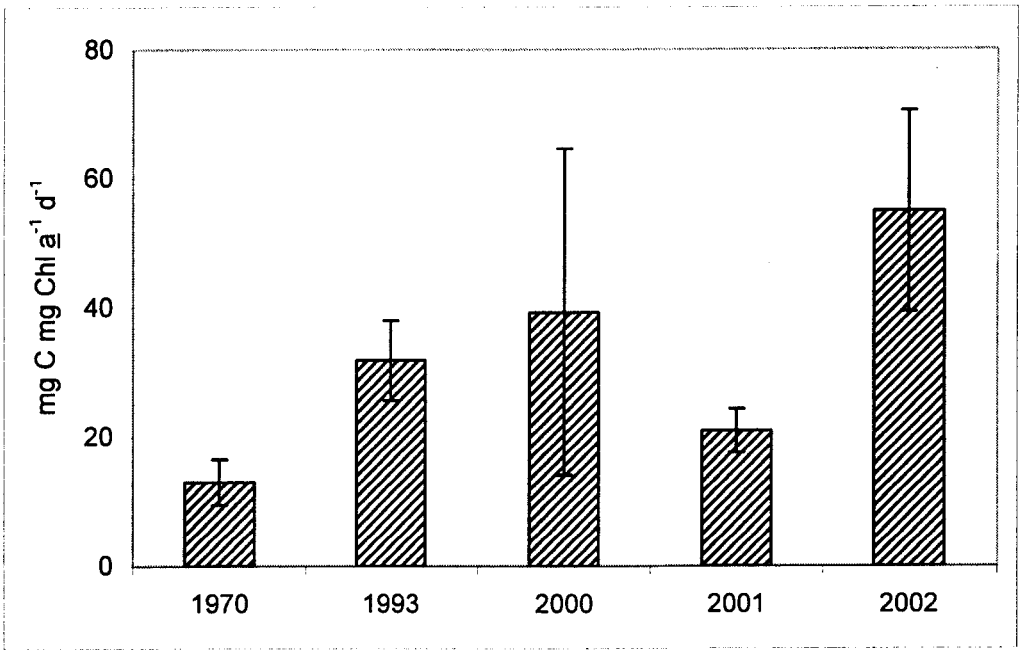


Figure 30a: June to September mean (+/- 1 S.E.) carbon assimilation rates, mg C mg Chl $\underline{a}^{-1}$ d^{-1}. 1970 data are from Glooschenko et al. (1974a; 1974b), 1993 data are from Dahl et al. (1995) and 2000-2002 data are from this study.

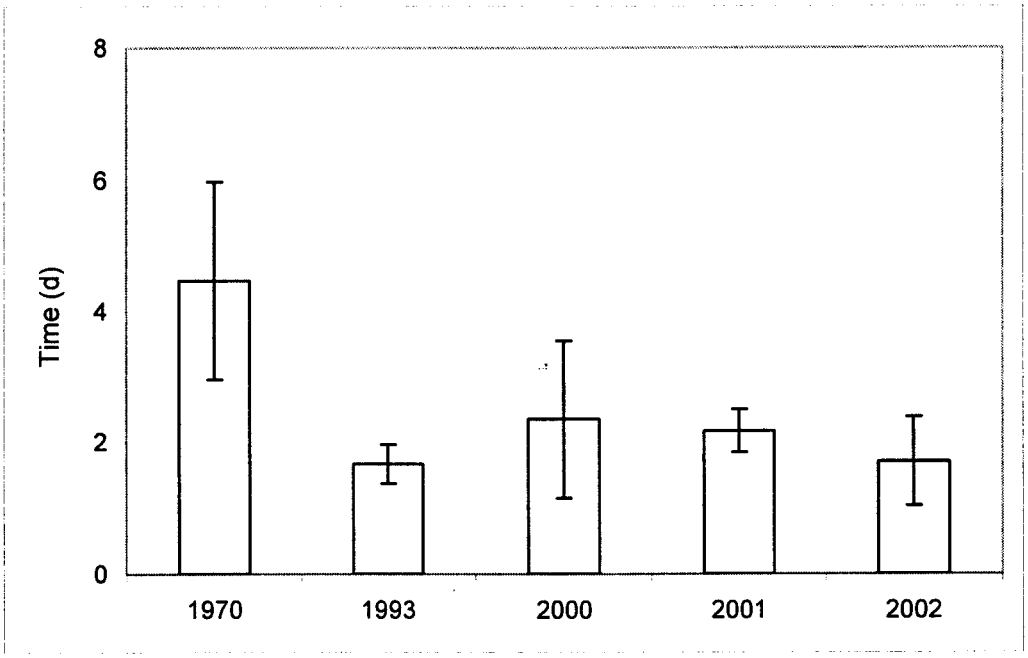


Figure 30b: June to September mean (+/- 1 S.E.) carbon turnover times, d. 1970 data are from Glooschenko et al. (1974a; 1974b), 1993 data are from Dahl et al. (1995) and 2000-2002 data are from this study.

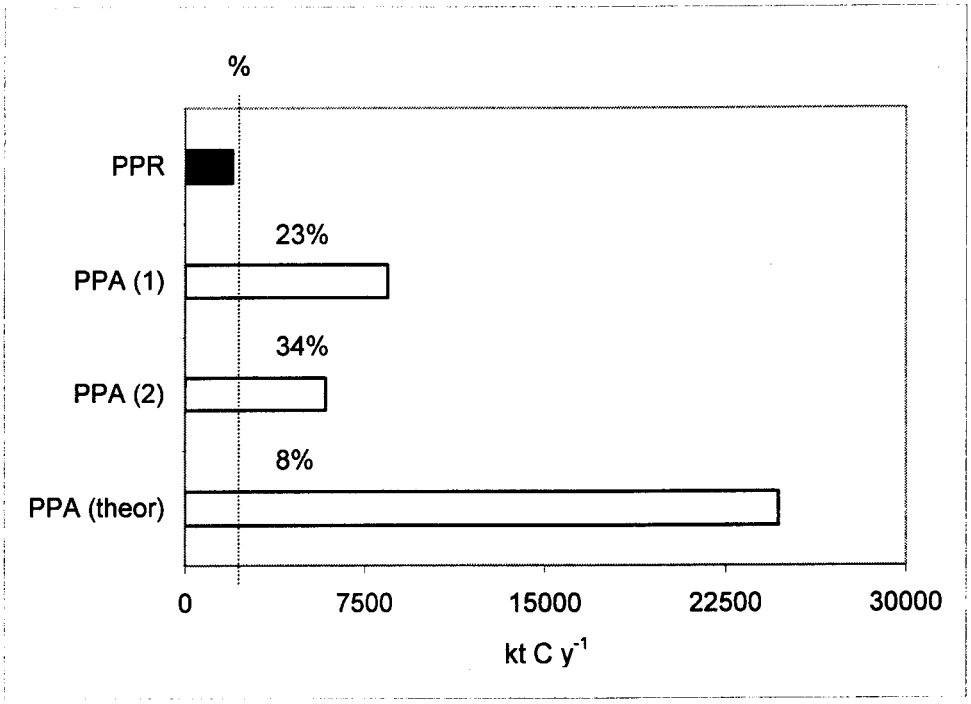


Figure 31: The lake-wide primary production required (PPR) to support a commercial catch of top predators compared to estimates of primary production available. Units are kt C y^{-1}. PPA (1) is biased high assuming that west basin data are applicable to all of Lake Erie. PPA (2) accounts for observed differences in primary production in the central and eastern basins. PPA (theor) is the theoretical level of primary production needed to sustain the catch at 1998 levels. Percentages (%) indicate the proportion of PPA consumed by PPR.

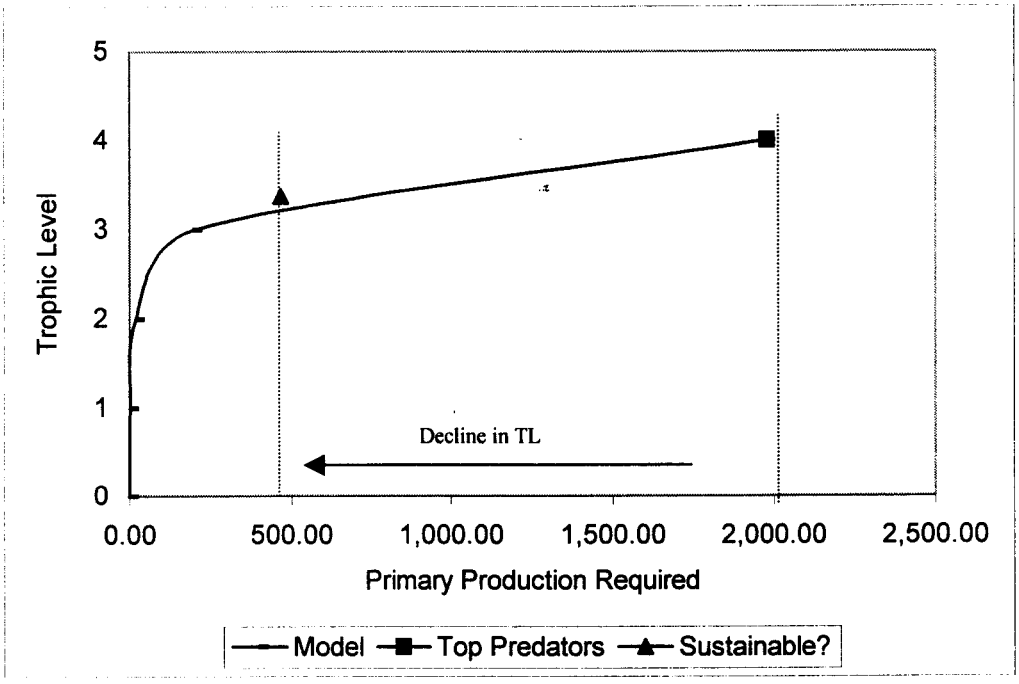


Figure 32: Illustrates the decline in average trophic level that is necessary to reduce PPR (kt C y^{-1}) and maintain a commercial catch of 17.8 million kg.

Conclusions

Primary production in western Lake Erie was measured by two different techniques, and in both cases there was no evidence that the rate of carbon fixation in the basin has changed over the past thirty years. Various models, including those of Vollenweider et al. (1974) have indicated that the primary production capacity of temperate lakes such as Erie will not exceed 420 g C $m^{-2}y^{-1}$. The original Vollenweider models predicted that this would decrease in Lake Erie as a result of phosphorus controls, yet this prediction was challenged by observations made during the current study. Despite the decrease in external phosphorus loadings from 6 g TP m^{-2} y^{-1} in 1970 to 1.4 g TP m^{-2} y^{-1} in 2000 that were mandated by the Great Lakes Water Quality Agreement, daily, seasonal and annual primary production estimates have not decreased. The role of internal phosphorus loadings in primary production dynamics warrants further investigation.

This study also demonstrated that the average trophic level of the commercial catch that can be sustained, lake wide, is 3.4. Top predators and prized commercial species such as walleye (*Stizostedion vitreum*), have a trophic level of 4 or higher. It is concluded that primary production estimates must be included in future fish management strategies.

Although primary production did not decrease, there have been significant declines in chlorophyll a, which suggested that the production potential of the western basin should have decreased. It is possible that with the observed increase in water clarity, phytoplankton photosynthesis now occurs deeper in the water column and thus overall areal rates of primary production have not changed. With increased clarity, the rate of

carbon fixation per unit chlorophyll a (the assimilation number) has more than doubled since 1970. The inverse of carbon assimilation is carbon turnover, and the doubling of carbon turnover rates since 1970 may have an important role in mitigating toxic stress.

An apparent paradox observed in this study was that although chlorophyll a concentrations have declined, there was no significant evidence of a decline in total algal biomass as measured as a function of cell counts and cell volumes. The latter technique revealed high variability based on the counting procedure and sampling limitations. It is conceivable, however, that changes in the algal community can change the ratio of chlorophyll a to cell volume. With the increase in water clarity, chlorophyll a to algal volume ratios would be expected to decline, but it was beyond the scope of this research to test this hypothesis. The algal community itself was showing signs of a structural change from the 1970s, with genera associated with oligotrophic conditions becoming more prevalent.

The contradiction between the two techniques used to estimate algal standing crop is sufficient to advise caution against the simple use of chlorophyll a as a reliable indicator. An accurate portrait of phytoplankton standing crop requires considerable expertise and a great deal of time. The few studies that have been undertaken in Lake Erie have been invaluable in increasing our understanding of the ecosystem, particularly within the context of eutrophication and exotic species invasions.

Finally, there is no doubt that the paucity of primary productivity and phytoplankton production information limits current management strategies in Lake Erie with regard to

both water quality and fishery management. Despite the endorsement of an ecosystem approach, there is little evidence that this approach has been adapted for the sustainable development of the natural resources of Lake Erie.

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